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TAXONOMIC SYNOPSIS OF *PITYOPSIS* (ASTERACEAE)

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ABSTRACT

A taxonomic synopsis of the genus *Pityopsis* recognizes 12 species, none with infraspecific taxa. Most USA populations west of the Mississippi River are treated as **Pityopsis tenuifolia** (Torrey) Nesom, **comb. et stat. nov.**, although typical *P. graminifolia* reaches eastern Arkansas, Louisiana, and eastern Texas. Plants in Mexico and Central America are identified as a disjunct segment of *P. graminifolia* sensu stricto. *Pityopsis adenolepis* is regarded as a synonym of *P. aspera*. *Pityopsis microcephala* is a distinct species of the Gulf and South Atlantic coastal plains. Comments on diagnostic features, a formal nomenclatural summary, and a county-level distribution map are provided for each species.

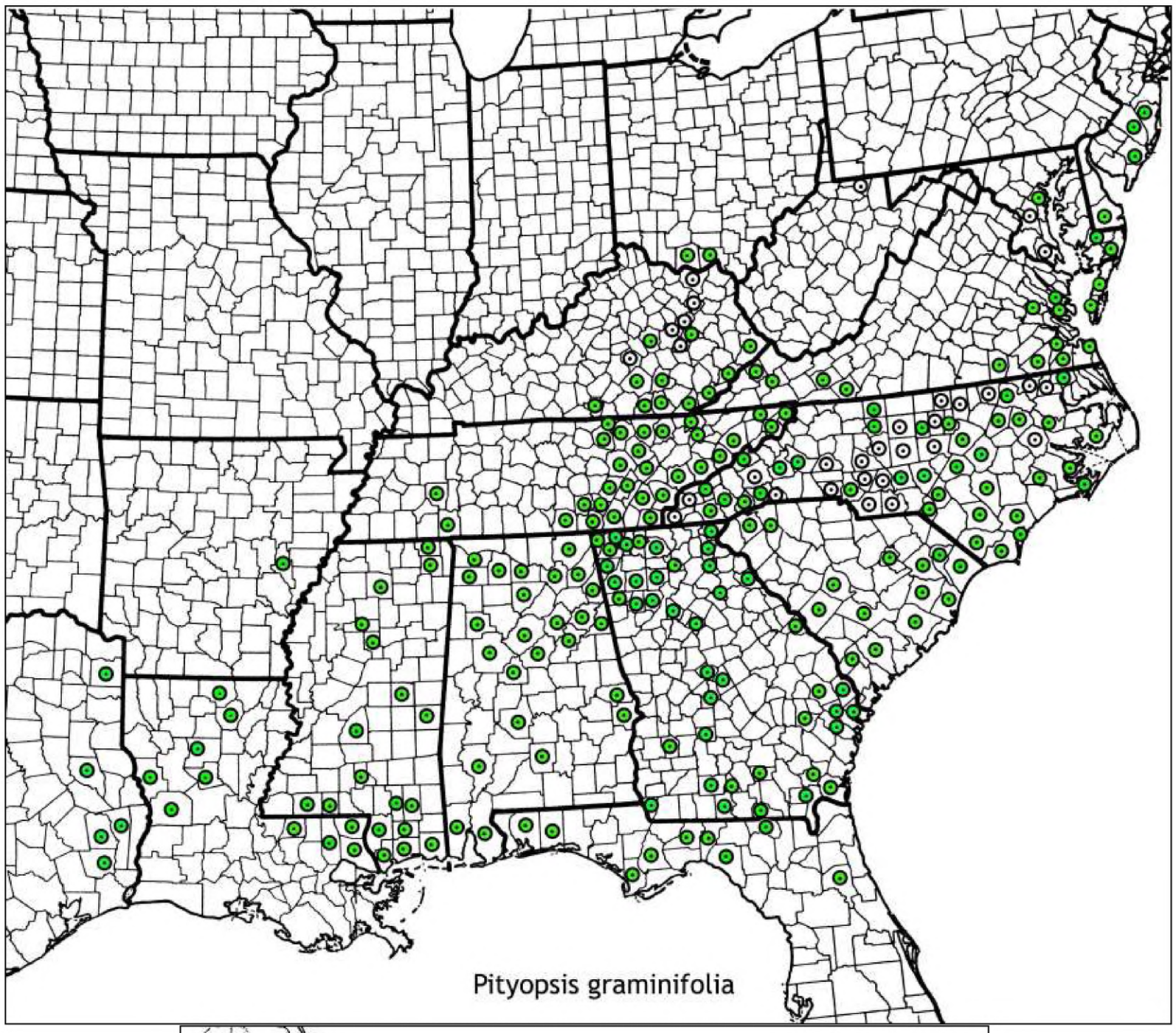
Interpretations of variation and associated nomenclature in *Pityopsis* Nutt. have varied (e.g., Small 1933; Fernald 1947, 1950; Dress 1953; Harms 1969; Bowers 1972; Cronquist 1980; Semple & Bowers 1985; Semple 2006; Weakley & Sorrie 2015). Recent taxonomic assessments of *Pityopsis* in the Florida peninsula (Bridges & Orzell 2018) have advanced an understanding of variation patterns within the genus –– from the variable matrix of *P. graminifolia* sensu lato, Bridges and Orzell recognized *P. aequilifolia*, *P. latifolia*, and *P. tracyi* as distinct species. With this potential resolution, remaining taxonomic problems and disagreements in the genus mainly involve variation in plants identified broadly as *P. graminifolia*, as *P. adenolepis* and *P. aspera*, and as *P. oligantha*. The present report provides a taxonomic summary of the genus as a whole, with hypotheses toward resolving these problems.

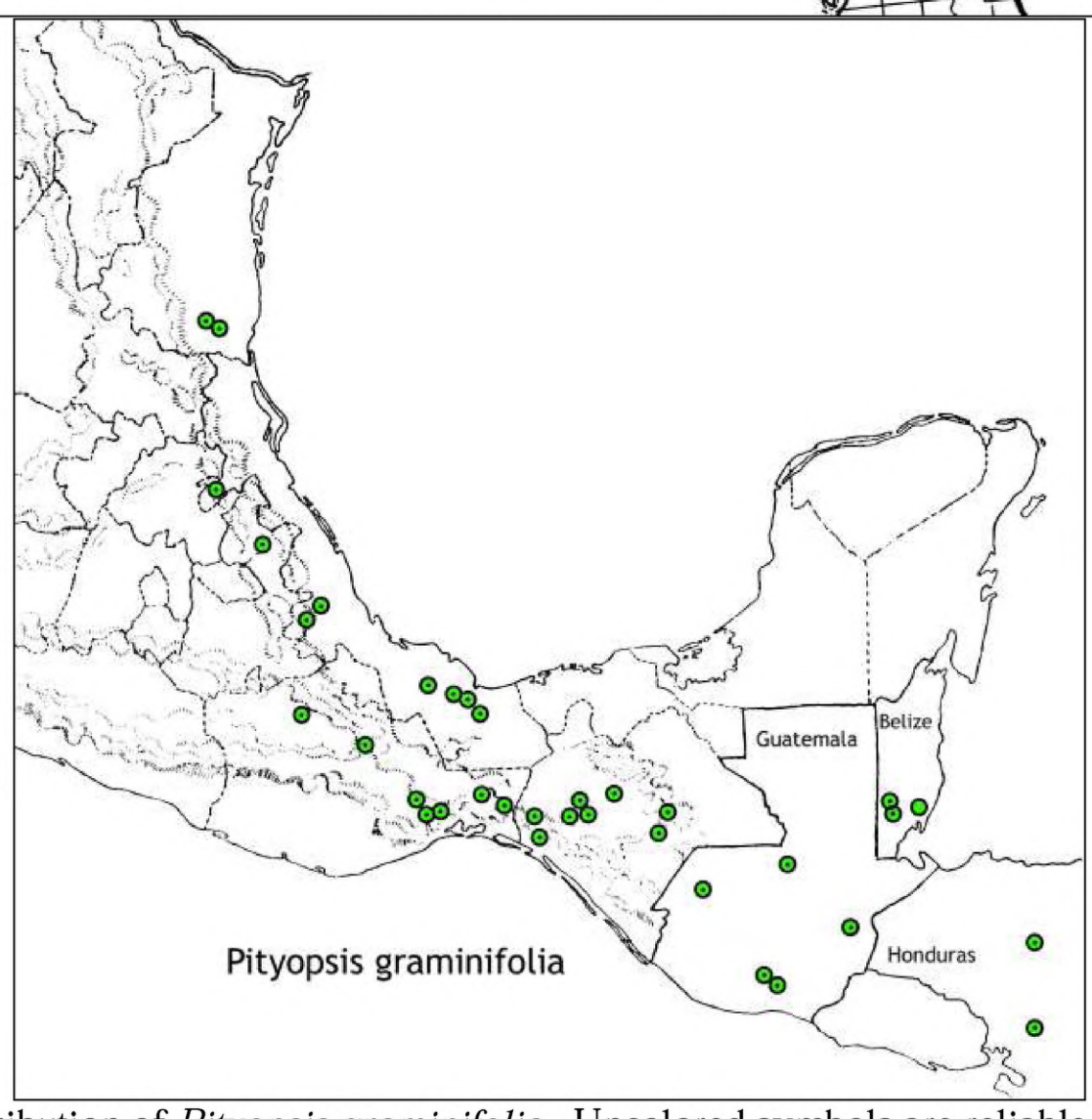
Classifications and phylogenetic analyses of *Pityopsis* (e.g., Semple & Bowers 1985; Gowe & Brewer 2005; Teoh 2008; Hatmaker 2016) are difficult to interpret because of inconsistences in identification and apparent inconsistencies in sampling of taxa. About the most that can be concluded with some confidence is that *P. falcata*, *P. ruthii*, and probably *P. pinifolia*, perhaps *P. flexuosa*, are components of one clade –– these are taxa that do not exhibit fire-dependent flowering (Gowe & Brewer 2005) and essentially comprise sect. *Pityopsis* of Semple and Bowers (1985), which they characterized by the absence of large basal rosette leaves at the time of flowering. Sect. *Graminifoliae* (Small) Semple of Semple and Bowers (1985) is typified by *P. graminifolia*.

PITYOPSIS Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 317. 1840. *Chrysopsis* [unranked] *Pityopsis* (Nutt.) Torr. & Gray, Fl. N. Amer. 2(2): 252. 1842. *Heterotheca* sect. *Pityopsis* (Nutt.) Harms, Wrightia 4: 9. 1968. **LECTOTYPE** (Pfeiffer, Nom. 2: 735. 1873): *Pityopsis pinifolia* (Ell.) Nutt.

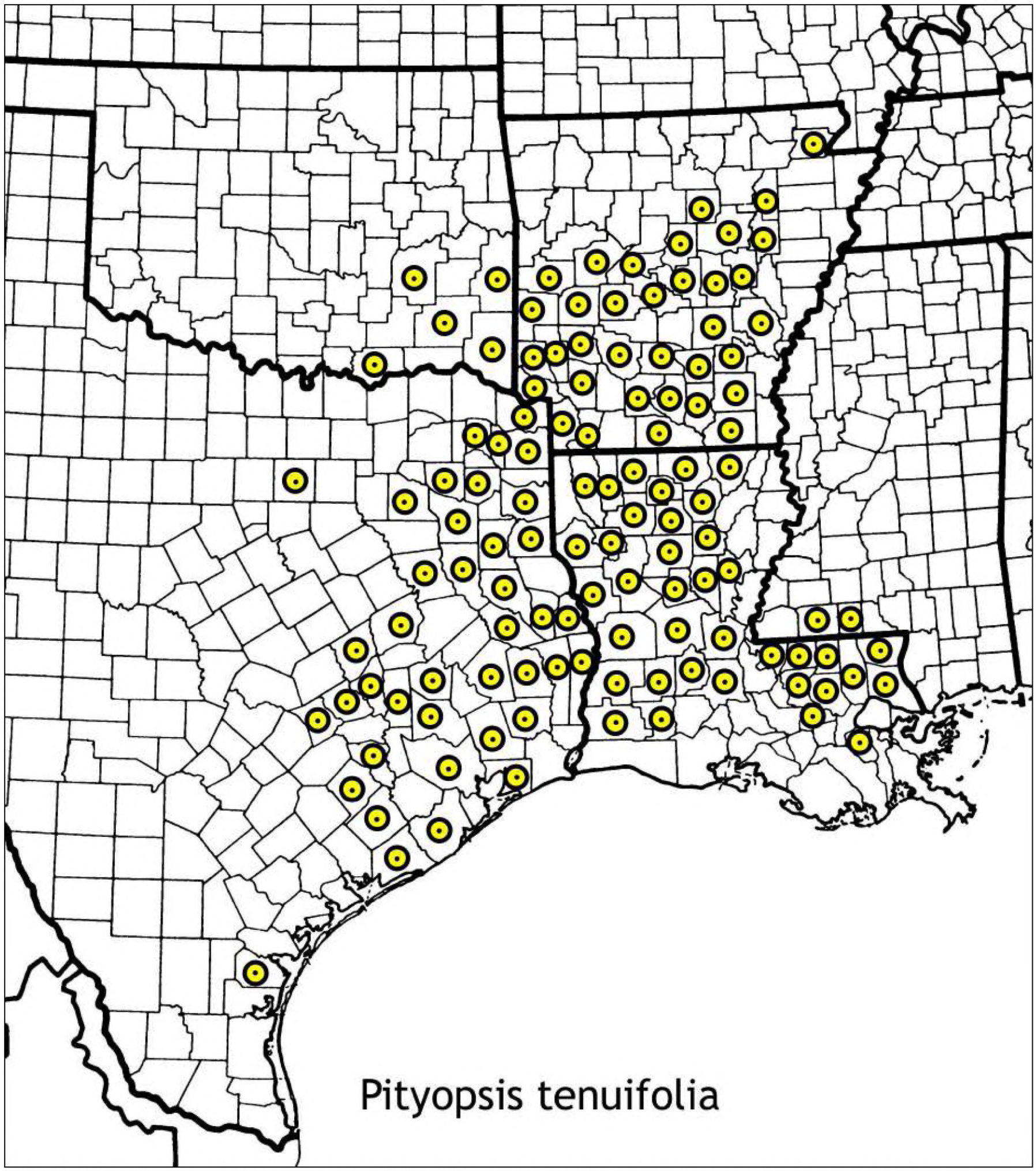
Heyfeldera Schultz-Bip., Flora 36: 35. 1853. **TYPE**: *Heyfeldera sericea* Schultz-Bip.

Herbaceous perennials, fibrous-rooted, usually with slender rhizomes or basal offsets. Indument silky-sericeous, of mostly appressed, anastomosing hairs, sometimes with stipitate glands. Leaves alternate, simple, entire, linear to linear-lanceolate or linear-oblanceolate, with parallel venation. Heads few to many in an open panicle; involucres turbinate; phyllaries in 4–8 graduated series. Ray corollas pistillate, fertile, yellow, coiling with maturity. Disc florets bisexual, fertile. Achenes of ray and disc similar, fusiform, loosely strigose; pappus of two series, the inner of barbellate bristles, the outer of much shorter setiform bristles or setae. Base chromosome number x=9.

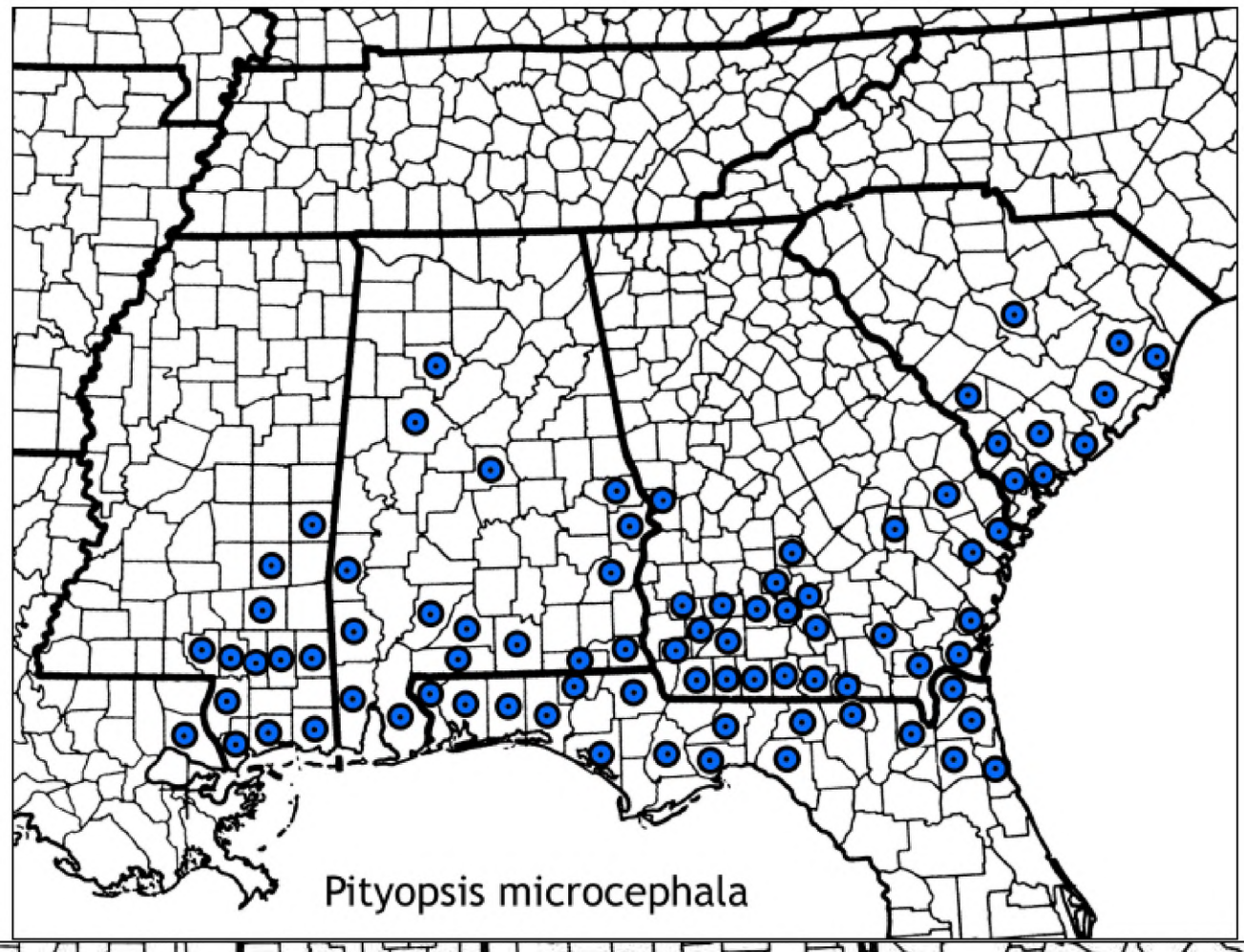


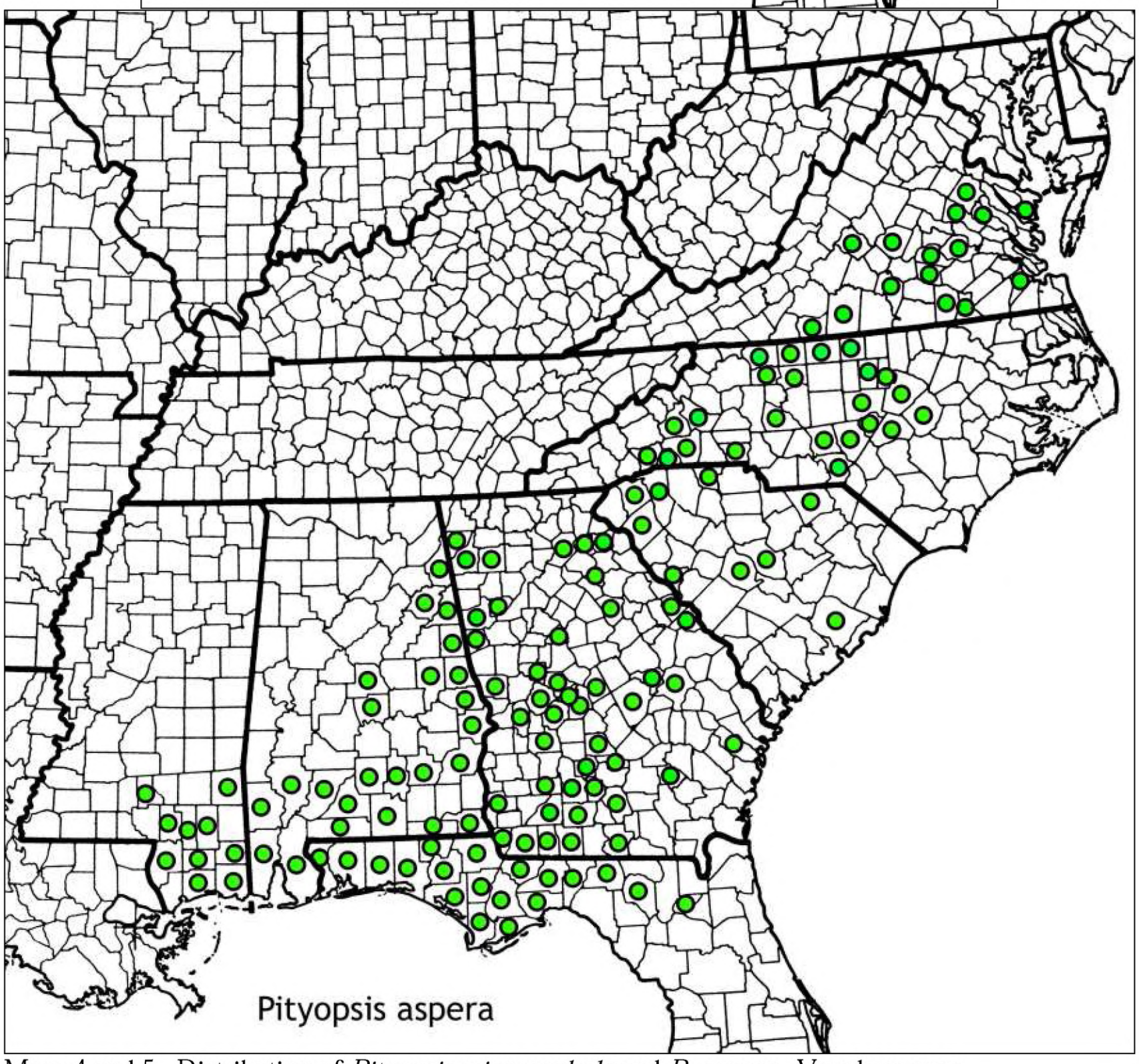


Maps 1 and 2. Distribution of *Pityopsis graminifolia*. Uncolored symbols are reliable records for which the author has not seen a voucher. The 'undotted' symbol in Belize perhaps is *P. tracyi* (text comments).

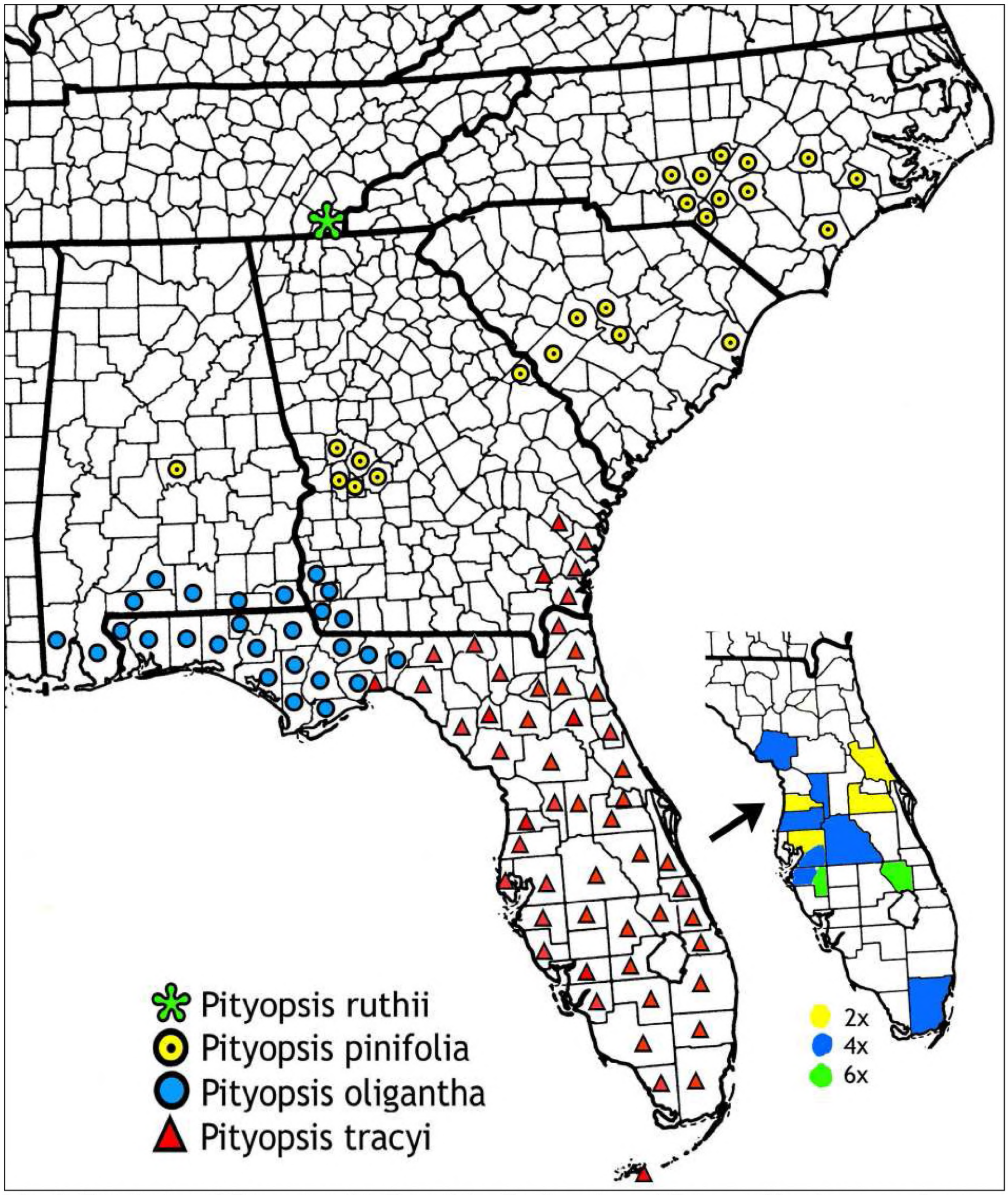


Map 3. Distribution of *Pityopsis tenuifolia*. Vouchers seen for most except a few in Arkansas.

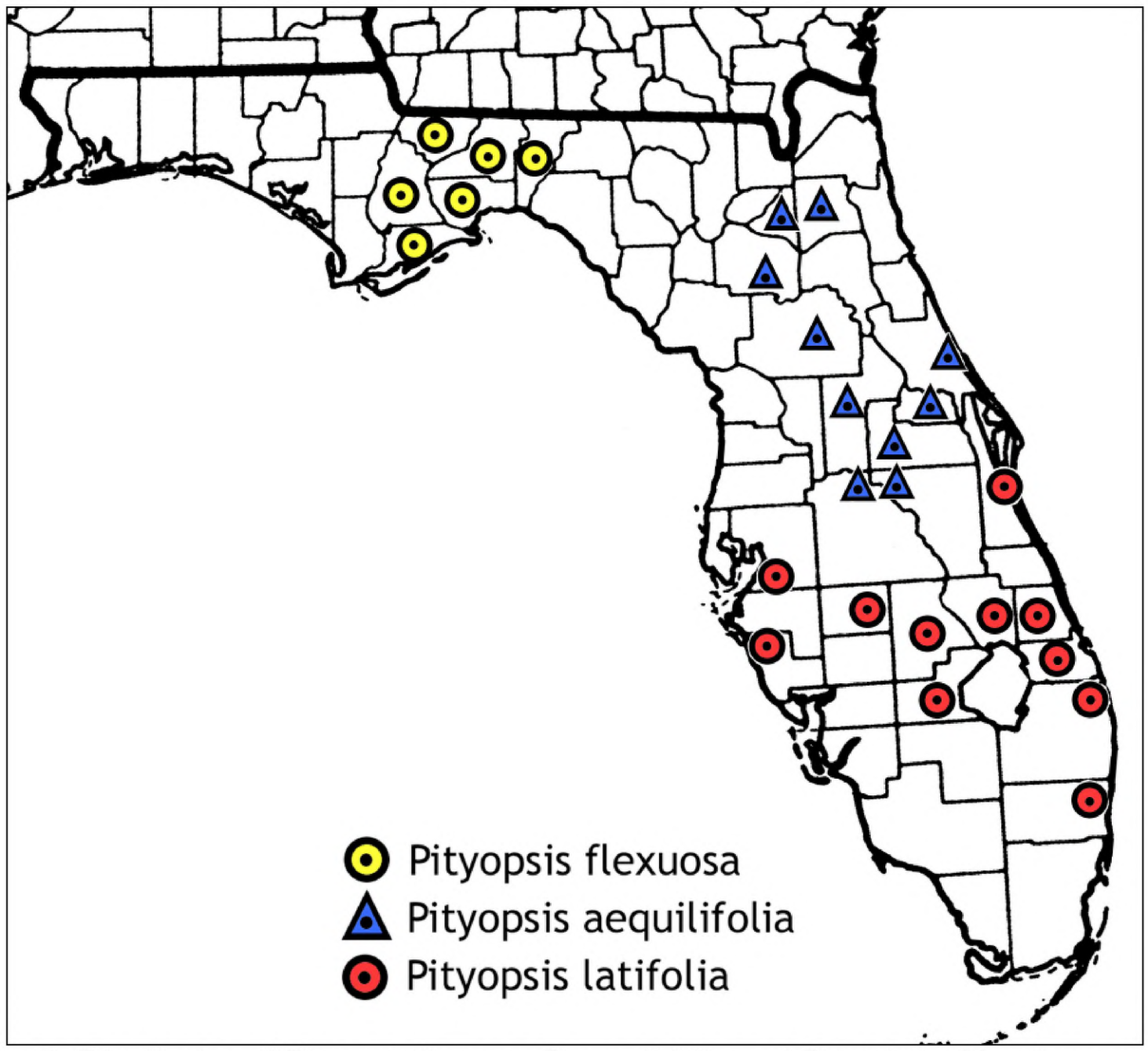




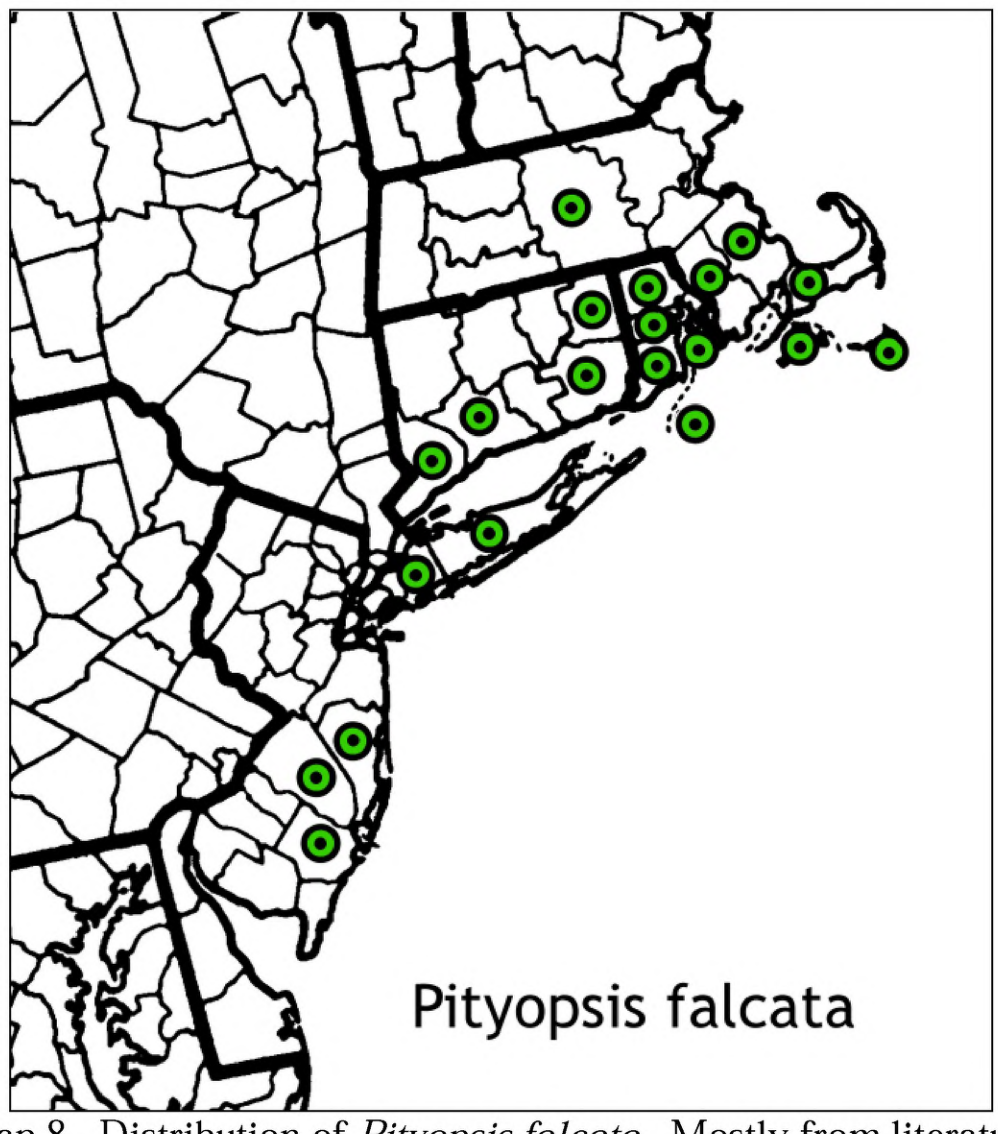
Maps 4 and 5. Distribution of *Pityopsis microcephala* and *P. aspera*. Vouchers seen.



Map 6. Distribution of *Pityopsis ruthii*, *P. pinifolia*, *P. oligantha*, and *P. tracyi*. Vouchers seen. Inset shows distribution of chromosome counts for *P. tracyi* (see text for data).



Map 7. Distribution of *Pityopsis flexuosa*, *P. aequilifolia*, and *P. latifolia*. Vouchers seen.



Map 8. Distribution of *Pityopsis falcata*. Mostly from literature.

1. Pityopsis aequilifolia (Bowers & Semple) Bridges & Orzell, J. Bot. Res. Inst. Texas 12: 31. 2018. *Pityopsis graminifolia* var. *aequilifolia* Bowers & Semple, Phytologia 58: 430. 1985. **TYPE**: **Florida**. Lake Co.: Tavares, sandy roadside on Fla Hwy 19, S of old US Hwy 441, 20 Sep 1971, *B.E. Wofford & F.D. Bowers 71-558* (holotype: TENN, image! in Bowers 1972). Map 7.

A distinctive species known from eight counties of north-central Florida. It is characterized by densely arranged, relatively broad and spreading (vs. narrow and closely appressed, as in *Pityopsis tracyi*), equal-sized cauline leaves, without enlarged, persistent basal leaves. Chromosome number diploid (citations below). Perhaps not distinct from *P. latifolia* (see comments following the latter).

Representative collections. **Florida**. Alachua Co.: Ashton Biological Research Station, 15 mi WSW of Gainesville, near Watermelon Pond, longleaf pine with *Quercus geminata* and *Q. incana*, 19 Oct 2001, *Carr 3964* (FLAS). Bradford Co.: 1.5 mi NW of Clay Co. line on Fla Hwy 100, 27 Oct 1978, Semple 4001, **2n=18** (USF). Clay Co.: ca. 8.1 air mi NW of Middleburg, ca. 1 air mi S of Duval Co. line, dry longleaf pine sandhills, 16 Oct 1992, *Orzell & Bridges 21159* (BRIT). Lake Co.: Fla Rte 19 ca. 7 mi S of jct with Fla Rte 20, sand pine scrub, 1 Nov 1978, *Godfrey 76863* (TTRS); ca. 5 air mi SE of Clermont, SW of powerline at dead end of unimproved road, 0.5 air mi S Hartwood Marsh Rd at a point 4.2 mi E of int US Hwy 27, overgrown longleaf pine-wiregrass sandhill and scrub, 8 Nov 1990, *Orzell & Bridges 15759* (FTG, TEX); 1 mi N of Altoona, deep sandy soil along RR, 27 Jul 1960, *Turner 4672* (SMU). Marion Co.: Rte 40 between Silver Springs and Rte 19, Ocala Natl Forest, dry sandy, sand pine scrub, 22 Nov 1980, *Gholson 8618* (FLAS); S of Juniper Spring Run, by Fla Rte 19, N of Fla Rte 40, S of Salt Spring, Ocala Natl Forest, sand pine-scrub oak sand ridge, 22 Nov 1980, *Godfrey 78274* (TTRS); 2.8 mi S of Salt Spring by Fla Rte 19, abundant in sandhill clearing (formerly sand pine scrub), 14 Oct 1987, *Godfrey 82582* (FTG); ca. 2 mi S of Salt Springs, Ocala Natl Forest, W side of FS Rd 65, 0.5 mi S of intersect. Fla Hwy 19, burned upland sandy longleaf pine savanna, 28 Apr 1990, *Orzell & Bridges 13272* (FTG); 9.6 km W of Juniper Springs on Hwy 40, Ocala Natl Forest, 1.0 km E of Forest Rd 579, edge of pine woods in road ROW, 23 Oct 1999, *Semple 10908*, **n=9II** (BRIT). Osceola Co.: 1 mi E of Loughman on Fla Hwy 54, dry open roadside, 7 Oct 1973, *Baltzell 5390* (FLAS). Polk Co.: Ca. 2.6 air mi E of the center of Davenport, W edge of Reedy Creek Swamp near mouth of Horse Creek, longleaf pine-turkey oak-wiregrass sandhill woodland, 12 Nov 1990, *Orzell & Bridges 15862* (FTG); ca. 1.3 air mi SE of the center of Davenport, W of Powerline Rd, just N of intersect. Snell Creek Rd, open, fire-maintained, disturbed sandhill, longleaf pine-turkey oak, 12 Nov 1990, *Orzell & Bridges 15885* (FTG, TEX); Davenport, sandy place, 20 Oct 1946, *Schallert 19882* (SMU); N of Withla on Co. Rd 33, 1.0 km S of Lake Co. line, disturbed sand, road ROW, 23 Oct 1999, *Semple 10905*, **n=9II** (BRIT, USF). Seminole Co.: 7.5 mi W of Sanford on Fla Hwy 46, sandy clearings in scrub, 2 Oct 1976, *Kral 59232* (VDB, VSC); ca. 4 mi SE of Sanford on US Hwy 17/92, weedy, moist, sandy margin of small pond in white sand Pinus clausa scrub, 28 Apr 1961, *Ray 10886* (USF); 5 mi S of Sanford, Hwy 17-92 at 5-Points, dry sandy field, 8 Jul 1966, *Scudder 7* (FLAS). Volusia Co.: [Daytona Beach], 1.4 mi S on Peninsula Drive from intersect. with Broadway St, sand pine grove, 30 Dec 1980, *Robinson 68* (USF).

2. Pityopsis aspera (Shuttlew. ex Small) Small, Man. S.E. Fl. 1341. 1933. *Chrysopsis aspera* Shuttlew. ex Small, Fl. S.E. US, 1182. 1903. *Heterotheca aspera* (Shuttlew. ex Small) Shinners, Sida 3: 348. 1969. **TYPE**: **Florida**. Leon or Wakulla Co.: Inter Tallahassee et St. Marks, in pinetis, Aug 1843, *F. Rugel 484* (holotype: NY; isotypes: HAL image!, K image!, US image!). Rugel's apparent collection number, "484," is on the US label but not the others. Map 5.

Chrysopsis graminifolia var. *aspera* A. Gray, Syn. Fl. N. Amer. 1(2): 121. 1884. **TYPE**: **Florida**. Leon or Wakulla Co.: Inter Tallahassee et St. Marks, in pinetis, Aug 1843, *F. Rugel 484* (holotype: NY image!; isotypes: HAL image!, K image!, US image!). In synonymy, Gray cited "(*C. aspera*, Shuttlew. in distrib. coll. Rugel)." In an account of Rugel collections from western Florida and Alabama, "Ch.[rysopsis] aspera Shuttl. n. sp." was listed in Bot. Zeit. 3:

221. 1845 -- as a nomen nudum, probably taken from the printed label of Rugel's distribution.

Chrysopsis adenolepis Fernald, Rhodora 44: 471. 1942. *Heterotheca adenolepis* (Fernald) Ahles, J. Elisha Mitchell Sci. Soc. 80: 172. 1964. *Pityopsis adenolepis* (Fernald) Semple, Canad. J. Bot. 58: 148. 1980. *Pityopsis aspera* var. *adenolepis* (Fernald) Semple & Bowers, Univ. Waterloo Biol. Ser. 29: 18. 1985. **TYPE**: **North Carolina**. Moore Co.: Pinehurst, old barren fields, 19 Aug 1897, *O. Katzenstein s.n.* (holotype: GH image!).

Harms (1969), Semple and Bowers (1985), and Semple (2006) treated *Pityopsis aspera* as including the typical form and *P. aspera* var. *adenolepis*. In the view of Semple and Bowers (following Bowers 1972 and Semple 1980, both of whom treated [*Chrysopsis*] *adenolepis* at specific rank), typical *P. aspera* is restricted to a small area of north-central Florida and adjacent Georgia and is diagnostically identified by stipitate-glandular peduncles, distal (and sometimes mid) stem portions, and margins of distal leaves. Plants identified as *P. adenolepis* or *P. aspera* var. *adenolepis* have involucres and a variable portion of the peduncles stipitate-glandular, but in contrast to *P. aspera*, faces of least distal leaves and most of the stem length are silky-sericeous; leaves rarely are glandular-margined.

In the view here, *Pityopsis aspera* is a distinctive species from Virginia southwest to Mississippi -- characterized by involucres, peduncles, and a variable portion of the stem length stipitate-glandular and without sericeous vestiture. Outer to inner phyllaries are triangular and usually coarsely stipitate-glandular along the whole length. Glands along margins of distal leaves are more common in Florida and southern Georgia than elsewhere in the range but a geographic boundary does not appear to be sharply defined and there is considerable variation in the number and density of marginal glands. The portion of stem/peduncle that is stipitate-glandular is variable, but nowhere in the range are the stems glandular completely to the base. *Pityopsis aspera* spreads colonially through short basal offsets as well as longer, slender rhizomes.

Diploid and tetraploid chromosome numbers have been recorded for *Pityopsis aspera* sensu lato (Semple & Bowers 1987). Following the maps in Semple and Bowers (1987, Figs. 2 and 3), diploids (including *P. aspera* sensu stricto of Bowers and Semple) are restricted to the coastal plain from North Carolina to Florida and apparently do not overlap in range with the tetraploids. A morphological difference that would consistently distinguish putative diploids from tetraploids is not evident.

3. Pityopsis falcata (Pursh) Nutt., Trans. Amer. Philos. Soc., n.s. 7: 318. 1840. *Inula falcata* Pursh, Fl. Amer. Sept. 2: 532. 1814 [1813]. *Inula mariana* var. *falcata* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 151. 1818. *Chrysopsis falcata* (Pursh) Ell., Sketch Bot. S. Carolina 2(4): 336. 1824 [1823]. *Heterotheca falcata* (Pursh) Harms, Castanea 34: 408. 1969 [1970]. **TYPE**: Protologue: "Herb. Banks. mss. In sandy pine-woods: New Jersey." **NEOTYPE** (Semple & Bowers 1985): **New Jersey**. No other locality data, 1836, *J. Torrey s.n.* (US, not seen). Map 8.

A distinctive species, especially in its glabrate, falcate leaves, eglandular involucres and peduncles, peduncular bracts few or none, and distinctly corymboid capitulescence above the level of the leaves. Plants are characteristically caespitose with a dense mass of fibrous roots, sometimes with basal offsets or short rhizomes. Chromosome number diploid (Semple & Bowers 1987). *Pityopsis falcata* is the northernmost species of the genus, ranging from Massachussetts to New Jersey.

A collection of *Pityopsis falcata* was reported from southeastern Canada by Cody (1952): **Ontario**. Along Canadian Natl Railway tracks W of Toronto, 25 Aug 1949, *Sharp s.n.* (DAO, not seen). It apparently was a waif at this locality.

A collection from Pinellas Co., Florida, cited by Semple and Bowers (1985) and Semple (2006) as *Pityopsis falcata* (St. Petersburg, along a beach, 1955, *O. Gunnison 2593*, herbarium not cited) probably is an unusual plant of *P. tracyi*, which is common in the area.

4. Pityopsis flexuosa (Nash) Small, Man. S.E. Fl., 1341. 1933. *Chrysopsis flexuosa* Nash, Bull. Torrey Bot. Club 23: 107. 1896. *Heterotheca flexuosa* (Nash) Harms, Castanea 34: 408. 1969[1970]. **TYPE**: **Florida**. Leon Co.: Bellair, 3 Sep 1895, *G.V. Nash 2545* (holotype: NY image!; isotypes: AC, E, F, FLAS, GH, K, MICH, MO, NDG, NEB, OS, P, US -- images of all!). Map 7.

A distinctive species endemic to six counties of northern Florida, characterized by eglandular involucres and peduncles, relatively large heads (involucres (7–)8–11 mm high), zigzag nodes, and crowded cauline leaves. Chromosome number diploid (Semple & Bowers 1987).

5. Pityopsis graminifolia (Michx.) Nutt., Trans. Amer. Philos. Soc. 2, 317. 1841. *Inula graminifolia* Michx., Fl. Bor.-Amer. 2: 122. 1803 (before 19 March, fide Schubert 1942). *Chrysopsis graminifolia* (Michx.) Ell., Sketch Bot. S. Carolina 2(4): 334. 1824 [1823], not *C. graminifolia* (Michx.) Nutt. ex Torr. & Gray 1842. *Diplopappus graminifolius* (Michx.) Less., Linnaea 5(1): 144. 1830. *Diplogon graminifolium* (Michx.) Kuntze, Revis. Gen. Pl. 1: 334. 1891. *Heterotheca graminifolia* (Michx.) Shinners, Field & Lab. 19: 71. 1951. **TYPE**: **USA**. No other collection data (probable holotype: P 00742815 image!; possible isotype: middle plant of P 00742818 image!, the 2 outer plants are *Pityopsis microcephala*). Maps 1 and 2.

Erigeron nervosus Willd., Sp. Pl., ed. 4, 3(3): 1953. 1803 (noted as 'in press' on 14 March, fide Schubert 1942). *Chrysopsis nervosa* (Willd.) Fern., Rhodora 44: 471. 1942. *Heterotheca nervosa* (Willd.) Shinners, Field & Lab. 19: 68. 1951. *Pityopsis nervosa* (Willd.) Dress, Baileya 19: 166. 1975. **TYPE**: **USA**. No locality data (B -- Bowers 1972 noted that he saw a photo). Protologue: "Habitat in America boreali.n 4 (v.s.) Caulis erectus pedalis simplex albo-tomentosus. Folia alterna inferiora quadri-pollicaria, summa semi-pollicaria et breviora, stricta rigida, lineari-lanceolata acuta integerrima nervosa viridia, subtus pilis sericeis adpressis albidis obsita. Panicula terminalis simplex, pedunculis tomentosis. Calyx imbricatus, squamis oblongis. Corollis non vidi. Pappus rufescens pilosus. W."

A plant in herbarium B-W (15682-01 0 image!) has an original label with "Am Sept, Desfontaines. W." -- it has small heads with eglandular peduncles and densely glandular involucres and unambiguously is *Pityopsis microcephala* (Small) Small.

Inula argentea Pers., Syn. Pl. 2(2): 452. 1807. *Chrysopsis argentea* (Pers.) Ell., Sketch Bot. S. Carolina 2(4): 334. 1824 [1823]. *Pityopsis argentea* (Pers.) Nutt., Trans. Amer. Philos. Soc., n.s. 7: 318. 1840. **TYPE**: **USA**. No collection data (P? not seen; Bowers (1972) indicated that he saw an "isotype" at L). Protologue: "Hab. in Pensylvania."

Haplopappus gramineus Benth., Pl. Hartw., 65. 1840. **TYPE**: **MEXICO**. **Oaxaca**. San Juan Reagi, July [1839], *K.T. Hartweg s.n.* (probable holotype: LD 1213502 image!).

Heyfeldera sericea Schultz-Bip., Flora 36(3): 36. 1853. **LECTOTYPE** (Semple & Bowers 1985): **MEXICO**. **Veracruz**. Mirador, Oct 1838, *J. Linden 1144* (K image!).

Chrysopsis correllii Fern., Rhodora 44: 470, t. 741, f. 1–2. 1942. *Heterotheca correllii* (Fern.) Ahles, J. Elisha Mitchell Sci. Soc. 80: 173. 1964. **TYPE**: **USA**. **North Carolina**. Bladen Co.: Sandy region at White Lake, 15 Jul 1935, *D.S. Correll 2577* (holotype: GH image!).

*Chrysopsis nervos*a var. *virgata* Fern., Rhodora 44: 474, t. 744, f. 1–2. 1942. **TYPE**: **USA**. **Virginia**. Nansemond Co.: NW of Magnolia, dry open sandy soil, 17 Oct 1941, *M.L. Fernald & B. Long 14036* (holotype: GH image!; isotypes: GH, NY, PH, US – images! of all).

Chrysopsis nervosa var. *stenolepis* Fern., Rhodora 44: 474, t. 743, f. 1–2. 1942. **TYPE: USA. North Carolina**. Pamlico Co.: Olympia, open woodland, moist soil, 12 Jul 1922, *L.F. & F.R. Randolph 910* (holotype: GH image!).

Pityopsis graminifolia is variable in habit (height, leaf size and shape) but consistent in its long, slender rhizomes, eglandular stems and peduncles, and relatively large heads with phyllaries glandular at least distally. The innermost series of phyllaries is unevenly longer than the next outer series and those phyllaries usually are thinner than the others (Fig. 1).

In North Carolina and Virginia, two widespread entities are present and distinct -- *Pityopsis graminifolia* and *P. aspera*. From South Carolina to Mississippi, with the relatively simple recognition of *P. aspera*, *P. oligantha*, and *P. pinifolia*, it is clear that two further entities remain -- one with small involucres and triangular, densely glandular phyllaries (*P. microcephala*) and one with larger involucres, the phyllaries narrowly oblong-lanceolate, slightly glandular, often mostly at the apices (*P. graminifolia*); Fig. 1 and key couplet below.

Figure 1. Representative involucres of *Pityopsis graminifolia* (left) and *P. microcephala* (right), at the same scale.

1. Involucres 8–10(–13) mm high, phyllaries linear-triangular (outer) to narrowly oblong-lanceolate (innermost), innermost series unevenly longer than the next outer series, inner to middle often glandular distally or only at the very apex, inner usually distinctly thinner; ray flowers 13–18 ..... **Pityopsis graminifolia**

1. Involucres 6–7 mm high; phyllaries all narrowly triangular, evenly imbricate in length, inner to outer all densely glandular the whole length (at least along the midregion), all similar similar in thickness; ray flowers 5–11 ..... **Pityopsis microcephala**

After study of a large set of collections from Mexico and Central America (at TEX-LL and UC-JEPS), no morphological features appear to unambiguously differentiate them from typical *Pityopsis graminifolia* of the eastern USA. Similarly, relatively uncommonly encountered populations in Louisiana, eastern Arkansas, and eastern Texas, within the range of *P. tenuifolia*, are identified here as *P. graminifolia*. Some of these plants have peduncles glandular a short distance beneath the involucres; the involucres are glandular only toward the apices of inner phyllaries, or all phyllaries may be sparsely glandular. The collection from Jasper Co., Texas (with glandular phyllaries and sparsely glandular distal peduncles), was originally identified as *P. oligantha* (Holmes & Singhurst 2012), and Semple and Bowers (1985) noted that a collection of *P. adenolepis* was made in Nacogdoches Co., Texas. Plants of *P. graminifolia* with similar vestiture occur in southwestern Mississippi, where the possibility exists that this might reflect introgression from *P. aspera*, but as noted by Bowers (1972, p. 105), similar plants also occur in Tennessee and Kentucky, where only *P. graminifolia* occurs. "These plants sometimes have glands on the peduncle which normally are hidden by pubescence but late in the year would be exposed giving a *H. adenolepis*-like peduncle."

Bowers observed that gene flow between *Pityopsis graminifolia* and *P. aspera* occurs in Virginia and in North and South Carolina, but "little of this introgression is seen in other areas even where the species may grow together." Observations in the present study suggest that gene flow between them also may occur across the Gulf Coastal Plain. In any case, however, most collections of *P. graminifolia* and *P. aspera* across their whole range are unambiguously identified as one or the other species.

Chromosome numbers tetraploid (inferred from mapped counts in North Carolina, Tennessee, and Virginia –– Semple & Bowers 1987, Fig. 5; other tetraploid counts are from Alabama and northern Florida, probably for *P. graminifolia*) and diploid (from East Feliciana Par., Louisiana, cited below). Hybridization between *Pityopsis graminifolia* and *P. aspera*, the latter apparently tetraploid over most of its range, would be expected to occur more commonly than between *P. graminifolia* and diploid species, except, perhaps, where *P. graminifolia* and *P. tenuifolia* are sympatric. A single hexaploid count (Etowah Co., Alabama, *Semple 6303*) has been made for *P. graminifolia* (Semple & Bowers 1987).

In Arkansas, Louisiana, and Texas, obvious intermediates between *Pityopsis graminifolia* and *P. tenuifolia* are uncommon or non-existent, although each apparently is diploid in that region. The two have different ecological preferences, with *P. graminifolia* characteristically in more moist or boggy habitats.

Collections of *Pityopsis graminifolia* where sympatric with *P. tenuifolia*. Arkansas. Prairie Co.: P.O. Hazen, rice prairie, never plowed, terrace deposits, 215 ft, 2 Oct 1966 *Demaree 54723* (NLU), *Demaree 54752* (SMU) at the same locality is typical *P. tenuifolia*. **Louisiana**. East Feliciana Par.: 5.6 km SE of Clinton, Idlewild Research Station, 15 Oct 1991, *Lievens 5095* (TEX); E of Woodland, La Hwy 432, 1.5 km E of La Hwy 67, road R-O-W in oak-pine, 13 Oct 1991, *Semple & Suripto 10113*, **n=9II** (NLU). Grant Par.: Ca. 5 mi W of Georgetown, old tower on Johns Hill Rd, pine uplands, 25 Oct 1966, *Thomas et al. 1069* (NLU); SW of Georgetown, seepage area in pine woods off Tabor Road, 31 Aug 1968, *Thomas et al. 12246* (NLU); SW of Georgetown, seepage area in longleaf pine woods near Tabor Road, 4 Oct 1970, *Thomas 21571* (NLU). Ouachita Par.: E of Luna at Claire Branch, S of Red Cut Loop Rd, baygall area under power line beside dirt road, 18 Sep 1991, *Thomas et al. 125,241* (NLU). Sabine Par.: 0.5 mi S of Many, clear-cut woods beside US Hwy 171, 4 Oct 1980, *Thomas 73,805* (NLU). St. Tammany Par.: Many collections. Tangipahoa Par.: Hammond, SLU campus, infrequent at North Campus Rec Complex, 25 Oct 1996, *Montz 8413* (NLU); 1/2 mi W of I-59, W of Fluker and just S of La Hwy 10, longleaf pine woods, 25 Oct 1974, *Thomas et al. 42155* (NLU); beside La Hwy 10 at I-55 W of Fluker, cleared pine woods, 28 Oct 1978, *Thomas et al. 62067* (NLU). Union Par.: Ca. 5.0 mi ENE of Conway, Union Wildlife Mgmt Area, clearcut along Old Tennessee Rd, 25 Sep 1983, *Moore 2697* (NLU). Vernon Par.: 1.5 mi ESE of Leesville, 1 mi E of Ft. Polk, Multi Purpose Range Complex, longleaf pine upland, 28 Oct

1997, *Keith s.n.* (NLU). Washington Par.: Many collections. Winn Par.: Ca. 1/2 mi E of Natchitoches Parish line, along KCS RR tracks and adjacent woods beside La Hwy 156, 20 Oct 1979, *Hutchinson & Carroll 294* (NLU); W of Winnfield on Hwy 84, 1.5 mi E of Gum Springs near Forest Service Rd 529, woods beside hwy at a creek, 25 Oct 1980, *Thomas 74419* (NLU). **Texas**. Cass Co.: Ca. 6.5 mi S of Bivins, sandy woods and seepage area, 18 Oct 1962, *Correll 26415* (LL). Hardin Co.: Village Creek State Park, E edge of Lumberton, 23 Oct 2003, *Sanders 6298* (BRIT, TEX). Jasper Co.: Kirbyville, Kirbyville Airport, periodically mowed area, 24 Sep 2000, *Holmes 11100* (BAYLU). Nacogdoches Co.: 1 mi S of Lone Pine Baptist Church, occasional in sandy soil next to road, 13 Oct 1976, *Cox 299* (BRIT); 6 mi E of jct Hwy 59 and FM 2664, creek area in pine-hardwood forest, 20 Oct 1976, *Nixon 7462* (BRIT); clear-cut logging site, *Schuster 221* (USFS, fide Semple & Bowers 1985, p. 20, identified by them as *P. aspera* var. *adenolepis* "out of the normal range ... and probably [representing] a chance introduction into the clear-cut logging tract site."). Tyler Co.: 2.5 mi N of Warren, infrequent in sandy soil above pitcher plant bog, 28 Sep 1948, *Cory 54904* (LL); Big Thicket Natl Preserve, E side of Turkey Creek Unit, Turkey Creek Pitcher Plant Bog/Savanna, on Pitcher Plant Trail, ca. 3.5 km S of FM 1943, 16 Oct 1997, *McRoberts 3715* (TEX); 6 mi N from Colmesneil on Hwy 69, pine-oak forest, 25 Sep 1988, *Suh 123* (TEX).

6. Pityopsis latifolia (Fern.) Bridges & Orzell, J. Bot. Res. Inst. Texas 12: 31. 2018. *Chrysopsis graminifolia* var. *latifolia* Fern., Bot. Gaz. 24: 434. 1897. *Chrysopsis latifolia* (Fern.) Small, Fl. S.E. US, 1182, 1339. 1903. *Pityopsis graminifolia* var. *latifolia* (Fern.) Semple & Bowers, Univ. Waterloo Biol. Ser. 29 (Rev. Pityopsis): 28. 1985. **LECTOTYPE** (Semple & Bowers 1985): **Florida**. [Martin Co.]: Jensen, sparse pine land, 25 Mar 1897, *A.H. Curtiss 5819* (GH image!; isolectotypes: GH image!, NY image!). Map 7.

As noted by Bridges and Orzell (2018, p. 28), *Pityopsis latifolia* is characterized by its "well-developed rosette of spreading to somewhat ascending, broadly strap-like basal leaves, typically over 2 cm wide, and its reduced, clasping cauline leaves. The inflorescence stalks are relatively short and stout, usually under 40 cm tall, and bear few heads. ... [It] flowers most profusely in the mid to late dry season (winter into early spring) and is therefore phenologically segregated from other members of *Graminifoliae* in the region [Atlantic Coastal Ridge], which flower in the late wet season into the early part of the dry season." Chromosome number diploid (citations below).

Pityopsis aequilifolia and *P. latifolia* are similar in their relatively large, densely arranged and even-sized cauline leaves, dense inflorescence of heads on short peduncles, and eglandular involucres, and both produce a woody, corm-like base and dense mass of fibrous roots, apparently without rhizomes. Diploid chromosome counts have been made for both. *Pityopsis latifolia* is distinct in its larger and persistent basal leaves, larger involucres, and phenology, and as considered here, the two species are allopatric (Map 7). They are so similar, however, and perhaps overlapping in morphology, that they should be investigated toward the possibility that only a single entity is represented. For specimens without basal parts, my identifications essentially have been based on geography, sorting them arbitrarily into northern and southern segments. Bowers (1972) and Semple and Bowers (1985) identified *P. graminifolia* var. *aequilifolia* as having a broader range on the Florida peninsula than mapped here, in part, apparently, because they included collections of *P. latifolia* sensu stricto. The two entities contrasted below, mostly following Bridges and Orzell (2018).

1. Involucres 5–9 mm high; disc florets 15–29; stem leaves dense, stiff and sharply pointed at apex; basal leaves narrow, similar to the cauline, usually not persistent ..... **Pityopsis aequilifolia**
1. Involucres 8–13 mm high; disc florets >30; stem leaves few, soft and obtuse or slightly acute at apex; basal leaves broadly oblanceolate, often persistent, narrowing to the cauline ..... **Pityopsis latifolia**

Broad-leaved plants of *Pityopsis tracyi* that might be confused with *P. aequililfolia* or *P. latifolia* produce slender, scale-leaved rhizomes and have a relatively slender caudex without densely

massed fibrous roots. Hybrids and introgressants, however, apparently are formed and identifications of such may be arbitrary (see comments following *P. tracyi*).

***Pityopsis latifolia*, representative collections**. **Florida**. Brevard Co.: N. Merritt's Island, 1.5 mi S of intersect. of Rte 3 and Happy Creek Rd, dry sandy soil near borrow pit on W side of Rte 3, 5 Feb 1973, *Shuey s.n.* (USF). Broward Co.: W of Ft. Lauderdale, 14 Feb 1931, *Bailey s.n.* (FLAS); 4 mi W of Deerfield, cut over pineland, 23 Feb 1941, *C. Deam 60848* (IND); S of Deerfield along ACL rights of way, *Pinus-Sabal* scrub in deep white sand, 21 Mar 1965, *Lakela 28333* (USF); 3 mi N of Pompano Beach, W of US Hwy 1, sand pine scrub, 20 Oct 1962, *Will s.n.* (FLAS). Glades Co.: Palmdale, plentiful on prairies, 7 Nov 1945, *Brass 15662* (Archbold); 3 mi W of Ortona on Hwy 78, scrub pine, 1 Nov 1969, *McCart 11,1196* (SMU). Hardee Co.: Highlands Hammock State Park, 13.5 mi E of Zolfo Springs, 8 mi W of Sebring, pine-oak scrub on white sand, 10 Nov 1978, *Hansen 4916* (USF). Highlands Co.: Lake June-in-Winter Scrub [Preserve State Park], Bobcat Trail, edge of flatwoods at edge of fire land, disturbed, 22 Oct 2002, *Bishop LJ0179* (USF); N side of Lake Annie, off of Rte 70 just W of Old State Rd 8, open sandy soil, 3 Sep 1981, *Correll 52397* (FTG); near Lake Josephine, Sebring, Sentinal Point Rd-Lake Josephine Dr, open pine sandhill, 29 Nov 1980, *Herndon 438* (FTG); ca. 3.5 air mi NE of Sebring, ca. 0.9 air mi S of Grassy Pond, ca. 0.75 air mi N of Carter Creek, ca. 2.3 air mi NE of jct Co Rds 17A and 700A (Arbuckle Creek Rd), white sand rosemary-scrub oak bald, 9 Nov 1990, *Orzell & Bridges 15796* (FTG, TEX); ca. 30 mi E of Arcadia along Rte 70, oak-pine scrub, sandy soil, 25 Apr 1951, *Webster 4213* (SMU). Hillsborough Co.: Rest area on Hwy 41, 0.7 mi S of [Little] Manatee River, sand pine-oak sandhill association, disturbed white sandy soil, 30 Sep 1976, *Semple 2501*, **n=9II** (USF). Martin Co.: N end of Jonathan Dickinson State Park, common in recently burned sand pine dunes, 28 Jul 1971, *Avery 995* (FTG); 5 mi W of Indiantown on State Rd 710, along RR tracks, 11 Nov 1968, *Keith & McCart 10265* (SMU); 9 mi NW of Umatilla by Fla Hwy 42, pineland sandhills, 10 Aug 1972, *Kral 48007* (VDB); just W of Jensen Beach, coastal dune scrub, 15 Aug 1972, *Kral 48079* (VDB); just W of Hobe Sound by US Hwy 1, sand pine scrub, 18 Sep 1973, *Kral 51772* (VDB); Stuart, dry sandy scrubland, 28 Dec 1954, Moldenke 21480 (SMU); ca. 0.9 air mi NW of Gomez, E of US Hwy 1, ca. 0.5 mi SE of jct Hobe Street, Atlantic Coastal Ridge scrub, 8 Mar 1993, *Orzell & Bridges 21259* (USF); Jonathan Dickinson State Park, pine woods near Casuarina campground, 10 Nov 1974, *Popenoe 295* (FTG); Jonathan Dickinson State Park, along edge of upper Kitchings Creek trail in moist prairie, 28 Jan 1979, *Popenoe 1584* (FTG); 2 mi W of Hobe Sound along US Hwy 2, sandy hills, 30 Nov 1974, *Turner & Plettman F45*, **n=9II** (FTG, LL). Okeechobee Co.: Okeechobee, pineland, 12 Oct 1941, *Davis s.n.* (FLAS); 1 mi E of Okeechobee City, low pineland, 7 Nov 1945, *West s.n.* (FLAS). Palm Beach Co.: Near West Palm Beach, sandy woods, 22 Feb 1904, *S. Deam 1710* (IND); northern city limits of Lake Park near US Hwy 1, around margins of saw palmetto and live oak scrubland, 8 Oct 1953, *Dress 2761* (FLAS); 1 mi N of Juno-Jupiter border off US Hwy 1, sand pine scrub, 3 Feb 1972, *Durako 48* (USF); Loxahatchee Wildlife Refuge off US Hwy 441 and due W of Lantana, slash pine-saw palmetto flats, 15 Nov 1984, *Kral 71686* (TENN); 1 mi S of Boynton Beach, pine-oak, white sand, 26 Dec 1967, *McCart et al. 35* (SMU); Boynton Beach at SW corner of I-95 and Hypoluxo Road, behind Grace Presbyterian Church, sand pine scrub, 30 Dec 1986, *Zona 150* (FLAS). Sarasota Co.: Sarasota, 23 Jan 1943, *Perkins s.n.* (USF). St. Lucie Co.: Inglehart Ranch, ca. 4 mi N of Martin Co. line, ca. 4.6 mi E of Okeechobee Co. line, edge of *Pinus clausa-Ceratiola ericoides* scrub in open sand, 12 Feb 1998, *Bradley & Woodmansee 890* (FTG); Rte 70, common in sandscrub, 26 Oct 1957, *Brass 29049* (Archbold Biol. Station); Savannas State Reserve, just N of Walton Rd, just W of FEC RR, disturbed scrub, 8 Nov 1995, *Gann & Bradley 211* (FTG); ca. 2-3 mi E of White City, sand dunes, 17 Sep 1964, *Kral 22862* (SMU); northern part of the county, E side of US Hwy 1, coastal sand scrub with *Pinus clausa*, 28 Jul 1962, *Lakela 25218* (FLAS); sand pine scrub, ca. 1 air mi NW of Walton, on ridge between FEC RR and "The Savannahs": Savannas State Reserve, sand pine scrub, 7 May 1990, *Orzell & Bridges 13375* (FTG, TEX); near Rio, scrub, 7 Jan 1923, *Small et al. 10776* (FLAS); Savannas State Reserve, S of Midway Rd (Co. Rd 712) N of Walton Rd, just W of RR tracks, disturbed open scrub, 5 Mar 1998, *Woodmansee 18* (FTG).

7. Pityopsis microcephala (Small) Small, Man. S.E. Fl., 1341. 1933. *Chrysopsis microcephala* Small, Fl. S.E. US, 1182, 1339. 1903. *Heterotheca microcephala* (Small) Shinners, Field & Lab. 19: 68. 1951. *Chrysopsis graminifolia* var. *microcephala* (Small) Cronq., Brittonia 29: 219. 1977. *Pityopsis graminifolia* var. *microcephala* (Small) Semple, Canad. J. Bot. 58: 148. 1980. **TYPE**: **Florida**. Duval Co.: Dry pine barrens near Jacksonville, 13 Oct 1894, *A.H. Curtiss 5319* (holotype: NY image!; isotypes: GH image!, K image!, US image!). Map 4.

Pityopsis microcephala is distinctive in its small heads (6-7 mm high, with 5-11 ray flowers), densely stipitate-glandular involucres, and eglandular peduncles. The phyllaries (outermost to inner) are consistently triangular-lanceolate and evenly imbricate –- the outermost (those at the involucre base) are densely congested and tiny, grading quickly in size into the primary 3-4 series. As noted by Semple and Bowers (1985), plants of the type collection are variable in the density of involucral glandularity, but even if this might reflect introgression from *P. graminifolia*, all of the type plants have the head size and involucral morphology of *P. microcephala*. Chromosome number diploid (inferred from mapped counts; Semple & Bowers 1987).

***Pityopsis microcephala*, collections seen, Louisiana**. St. Tammany Par.: Ca. 3.5 mi ENE of Abita Springs along La Hwy 435, undeveloped areas behind Hillcrest subdivision, weedy, roadside ditch bordering pine woods, 17 Sep 1981, *Pruski 2142* (TEX); La Hwy 434, ca. 1.5-2 mi S of jct with US Hwy 190 in Lacombe, weedy roadside along pine woods, 13 Oct 1981, *Pruski 2206* (TEX); pine forest next to West Gate Rd, N of Transportation Rd, 30 Sep 1994, *Slaughter 5629* (TEX).

8. Pityopsis oligantha (Chapm. ex Torrey & Gray) Small, Man. S.E. Fl.,1341. 1933. *Chrysopsis oligantha* Chapm. ex Torrey & Gray, Fl. N. Amer. 2(2): 253. 1842. *Heterotheca oligantha* (Chapm. ex Torrey & Gray) Harms, Wrightia 4: 11. 1968. **LECTOTYPE** (Semple & Bowers 1985): **Florida**. Damp barrens, April and May, *Dr. Chapman s.n.* (NY 163244 image!; isolectotypes: NY 163244 and 163245 images!; probable isolectotypes: GH 55871, 55872, and 55873 images!, K image!, NY 163238 and163246 images!, PH image!, US 652187, bearing 2 collections, image!, YU image!). Protologue: "Damp pine barrens of Middle Florida." Map 6.

A distinctive species endemic to panhandle Florida and adjacent counties of Georgia and Alabama, characterized by few heads on sparsely leafy stems (the basal leaves persistent) and glandular involucres and peduncles. Plants often develop a lignescent, fibrous-rooted caudex but characteristically produce long rhizomes. Habitats of *Pityopsis oligantha* are distinctly wetland and it is characteristically spring-flowering. Chromosome number tetraploid (Semple & Bowers 1987). A report of the occurrence of *P. oligantha* in Texas (Holmes & Singhurst 2012) was based on a collection of plants recognized here as *P. graminifolia*. Collections from Mississippi identified as *P. oligantha* (*Rogers 45468* image! – Pearl River Co. and *Gordon 1548* image! – George Co., both at MMNS) instead have proved to be *P. aspera*.

9. Pityopsis pinifolia (Ell.) Nutt., Trans. Amer. Philos. Soc., ser. 2, 7: 318. 1840. *Chrysopsis pinifolia* Ell., Sketch Bot. S. Carolina 2(4): 335. 1824 [1823]. *Diplogon pinifolium* (Ell.) Kuntze, Revis. Gen. Pl. 1: 334. 1891. *Heterotheca pinifolia* (Ell.) Ahles, J. Elisha Mitchell Sci. Soc. 80: 173. 1964. **NEOTYPE** (Semple & Bowers 1985): **Alabama**. No other data, *S. Elliot s.n.* (NY 00163185 image!). Map 6.

A distinctive and morphologically unmistakable species, especially in its glabrate, linear-filiform leaves, with scattered populations and population clusters from central Alabama (Autauga Co.: 6 Jun 1995, *Oberholtzer s.n.*, AUA-image!) to southeastern North Carolina. Chromosome number diploid (Semple & Bowers 1987). Spreading colonially by long, slender rhizomes.

10. Pityopsis ruthii (Small) Small, Man. S.E. Fl. 1341. 1933. *Chrysopsis ruthii* Small, Bull. Torrey Bot. Club 24: 493. 1897. *Heterotheca ruthii* (Small) Harms, Castanea 34: 408. 1969 [1970]. **TYPE**: **Tennessee**. Polk Co.: Hiawassee Valley, rocks, Oct 1896, *A. Ruth 7* (holotype: NY image!; isotypes: NCU image!, OS image!). Ruth's label on the OS sheet specifies "rocks at McFarland." Map 6.

A distinctive species endemic to rocky habitats along the Hiawasee and Ocoee rivers in Polk Co., Tennessee. Involucres and peduncles stipitate-glandular, otherwise glabrous. Chromosome number diploid (Semple & Bowers 1987). Because of its restricted geography and rarity, it has been the subject of autecological, ecological, and genetic studies (e.g., Farmer 1977; Thomson & Schwartz 2006; Moore et al. 2016; Hatmaker et al. 2018; Wadl et al. 2018).

11. Pityopsis tenuifolia (Torrey) Nesom, **comb. et stat. nov.** *Inula graminifolia* var. *tenuifolia* Torrey, Ann. Lyceum Nat. Hist. New York 2: 212. 1827. *Pityopsis graminifolia* var. *tenuifolia* (Torrey) Semple & Bowers, Univ. Waterloo Biol. Ser. 29 (Rev. Pityopsis): 24. 1985. **TYPE**: No collection data cited in the protologue but probably this: **Oklahoma** (one of the southeastern counties). Long Expedition, early Sep 1820, *E.P. James s.n.* (holotype: NY image!). The Long Expedition (1819-1820, with James as botanist, see Torrey 1827) reached Fort Smith, Arkansas (the expedition's endpoint), on 13 September 1820, after traveling through the Texas panhandle region and across southern Oklahoma. Map 2.

Pityopsis tenuifolia is distinctive in its slender rhizomes, eglandular vestiture (peduncles, involucres), closely ascending cauline leaves, minute, densely arranged peduncular bracts grading into the outer (basal) phyllaries, involucres 8–11 mm high with linear-triangular, evenly imbricate phyllaries, and ray florets 7–9 mm long. Chromosome number diploid (inferred from mapped counts in Arkansas, Louisiana, and Texas; Semple & Bowers 1987, Fig. 5). It is similar to *P. tracyi* in most features but is consistent in chromosome number and is less variable in morphology. Their disjunct geography and a consistent difference in achene morphology support recognition of *P. tenuifolia* at specific rank.

1. Achenes 2.5–3 mm long, with 7–8 prominently raised, resinous veins ..... **Pityopsis tenuifolia**
1. Achenes 2.5–4 mm long, without raised veins, or if veins slightly raised then not resinous ..... **Pityopsis tracyi**

***Pityopsis tenuifolia*, collections seen, Mississippi**. Amite Co.: South Greensburg Road at Mary Wall Bridge Road S of Liberty, school lands, 28 Sep 1998, *Alford 94* (MISS); 15 mi N of Liberty, pinelands, 16 Oct 1973, *Westbrook s.n.* (LSU). Pike Co.: Hwy 570 NE of McComb, near jct with River Rd, 13 Oct 2012, *Sullivan 12.4752* (MMNS); along W bank of Bogue Chitto River at the US Hwy 98 bridge SE of McComb, 12 Oct 1996, *Thomas 152,957* (TENN).

12. Pityopsis tracyi (Small) Small, Man. S.E. Fl., 1341. 1933. *Chrysopsis tracyi* Small, Fl. S.E. US, 1182. 1903. *Heterotheca graminifolia* var. *tracyi* (Small) Long, Rhodora 72: 43. 1970. *Pityopsis graminifolia* var. *tracyi* (Small) Semple, Phytologia 58: 430. 1985. *Pityopsis nervosa* var. *tracyi* (Small) Ward, Novon 14: 368. 2004. **TYPE**: **Florida**. Manatee Co.: Palma Sola, 3 Dec 1901, *S.M. Tracy 7713* (holotype: NY image!; isotypes: F image!, GH image!, US image!). Map 6.

Pityopsis tracyi is "a very distinct species and the most common member of section *Graminifoliae* in central and south-central Florida" (Orzell & Bridges 2018, p. 31). It occurs into counties of southeastern Georgia as well as in the Bahamas and perhaps in Belize in Central America (see citations below).

"*Pityopsis tracyi* is a robust, large-flowered species that is locally abundant in somewhat poorly to poorly drained pine savannas and seasonally wet grasslands with a historical high fire return interval (annual or biennial) from lightning season fires. Within the C4 grass-dominated groundcover matrix of these savanna-grasslands, *P. tracyi* often forms clonal patches from its elongated and branched underground rhizomes, which enable it to rapidly resprout after fires. A single genet is capable of occupying an area several meters in diameter" (Bridges & Orzell 2018, p. 31).

Cauline leaves of *Pityopsis tracyi* are usually linear to linear-triangular, usually ascending close to the stem; involucres and peduncles eglandular; involucres 7–14 mm high; phyllaries evenly imbricate in length, linear-triangular with a linear apex, usually loosely strigose-hirsute from base to tip. A relatively unelaborated caudex and long, slender rhizomes distinguish *P. tracyi* from *P. aequilifolia* and *P. latifolia*, which occur in sympatry.

Plants of the type collection of *Pityopsis tracyi* (Fig. 2) produce long, persistent basal leaves and both the basal leaves and the cauline leaves are nearly filiform. Plants of similar morphology are relatively common in southern counties of the peninsula (especially Dade, Collier, Hendry, Lee, and Monroe counties, where *P. tracyi* is the only species present), but Figures 2-14 show a range of variation in the habit of the species. Stem height, the number and density of cauline leaves, and the number and size of heads are variable.

Diploid, tetraploid, and hexaploid chromosome numbers have been recorded for *Pityopsis tracyi* (all within Florida), but a clear geographic pattern (see Map 6, inset) is not evident in the collections I have studied. **Diploid (2n=18)**: Hernando Co., *Semple 2559* (USF); Hillsborough Co., *Semple 2529* (USF); Orange Co., *Semple 2*556 (USF); Volusia Co., *Semple 2540* (USF). **Tetraploid (2n=36)**: Dade Co., *Turner F-33* (LL); Hillsborough Co., *Semple 5406* (USF); Levy Co., *Semple 3953* (cited by Semple & Bowers 1987 as *P. graminifolia*); Manatee Co., *Semple 5411* (cited by S&B 1987 as *P. graminifolia*); Pasco Co., *Semple 5416* (cited by S&B 1987 as *P. graminifolia* var. *latifolia*); Polk Co., *Semple 7484* (cited by S&B 1987 as *P. graminifolia* var. *latifolia*); *Semple 10904* (USF); Sumter Co., *Semple 3977* (USF). **Hexaploid (2n=54)**: Manatee Co., *Semple 5410* (cited by S&B 1987 as *P. graminifolia* var. *tracyi*); Okeechobee Co., *Semple 7514* (cited by S&B 1987 as *P. graminifolia* var. *tracyi*).

Bridges and Orzell (2018, p. 31) observed that a fourth species of *Pityopsis* (apart from *P. aequilifolia*, *P. latifolia*, and *P. tracyi*) occurs in central and southern Florida –– "a short, small-headed species with very narrow leaves ... restricted to well-drained sandhills with an open canopy of *Pinus palustris* or *Pinus densa*" –– identified by them as *P. microcephala*. As identified here, these plants (fide a photo by Edwin Bridges from a Highlands County population) are a very small-headed form of *P. tracyi* –– similarly small-headed plants (involucres 7–8 mm high and with relatively few phyllaries) occur at least in Okeechobee and Seminole counties (pers. observ.). Edwin Bridges (pers. comm.) notes that the small-headed Highlands County plants were discontinuous in morphology from others (larger-headed) at the same locality. It seems plausible that differences in chromosome number may underlie the apparent reproductive isolation.

Some of the chromosome number variants may be hybrids and introgressants among *Pityopsis tracyi*, *P. aequilifolia*, and *P. latifolia* and identifications (to species) of the polyploids may sometimes be arbitrary. For example, in Levy County, typical *P. tracyi* is known to occur (Fig. 11), but morphological variants also have been collected –– Figs. 12 and 13 show rhizomatous plants with densely arranged, relatively broad cauline leaves suggestive of *P. aequilifolia*; Fig. 14 shows a densely fibrous-rooted plant with narrow leaves characteristic of *P. tracyi*.

***Pityopsis tracyi*, representative collections. Georgia**. Brantley Co.: Hwy 82, 6.0 mi W of jct US Hwy 301 in Nahunta, open sandy area along and N of hwy, 21 Sep 1991, *Carter 9222* (VSC). Camden Co.: Ca. 11.75 air mi NNE of St. Mary's waterfront Cabin Bluff preserve, 0.76 mi W of Shellbine, cutover

Figure 2. *Pityopsis tracyi*, US isotype. Manatee Co., Florida.

Figure 3. *Pityopsis tracyi*. Manatee Co., Florida

Figure 4. *Pityopsis tracyi*. Hillsborough Co., Florida. *Semple 5406*, voucher for tetraploid chromosome count.

Figure 5. *Pityopsis tracyi*. Hillsborough Co., Florida.

Figure 6. *Pityopsis tracyi*. Hillsborough River State Park in Hillsborough Co., Florida. *vanHoek & Petty HR0407* (USF). The left plant is typical in morphology; the right plant perhaps is *P. latifolia* (basal portions critical for ID). Alternatively, the two might simply be populational variants, or the right plant might be introgressed with genes of *P. latifolia*, perhaps a ploidal variant (see text).

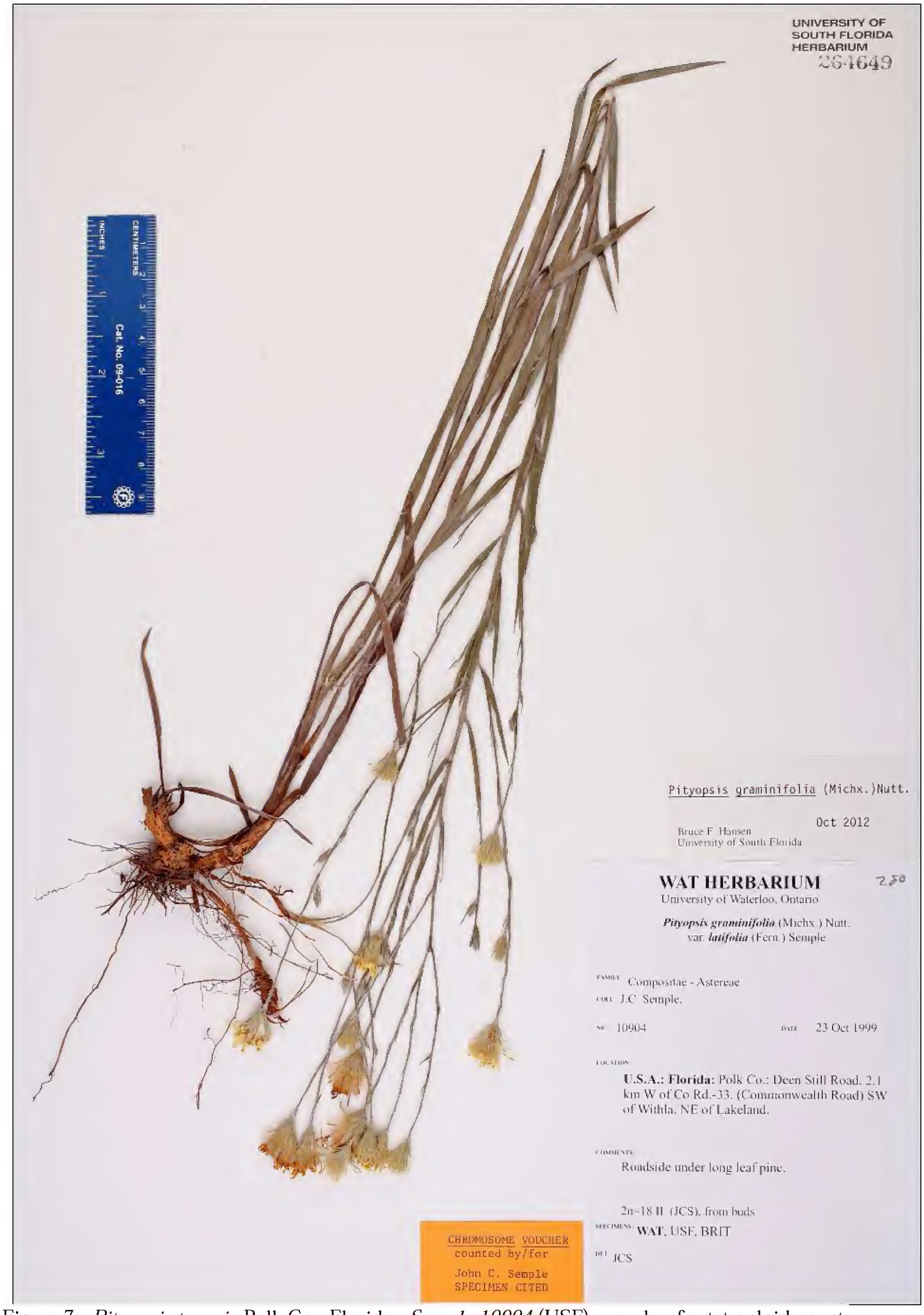


Figure 7. *Pityopsis tracyi*. Polk Co., Florida. *Semple 10904* (USF), voucher for tetraploid count.

Figure 8. *Pityopsis tracyi*. Polk Co., Florida.

Figure 9. *Pityopsis tracyi*. Polk Co., Florida.

Figure 10. *Pityopsis tracyi*. Polk Co., Florida.

Figure 11. *Pityopsis tracyi*. Levy Co., Florida. Typical morphology.

Figure 12. *Pityopsis tracyi*. Levy Co., Florida. Rhizomatous, perhaps introgressed from *P. aequilifolia*.

Figure 13. *Pityopsis tracyi*. Levy Co., Florida. Rhizomatous, introgressed from *P. aequilifolia*.

Figure 14. *Pityopsis tracyi*. Levy Co., Florida. Apparently without rhizomes, perhaps introgressed from *P. aequilifolia*. Note viviparous head (arrow); viviparous heads on *P. tracyi* also have been observed in Pinellas Co. (*Wunderlin et al. 10357*, USF).

flatwoods, 16 Sep 1995, *Carter 12789* (VDB). Glynn Co.: S tip of Jekyll Island, ca. 0.1 mi W of beach and 3 mi NNE of Jekyll Point, abundant on open, mostly stabilized dunes, 11 Sep 1974, *Duncan 29116* (TEX, VDB); S tip of Jekyll Island, ca. 1 mi NE of Jekyll Point, stabilized dunes, 13 Oct 1975, *Duncan 29648* (GA); Jekyll Island, sand dunes near picnic area, 9 Aug 1977, *Jones & Coile INPR38* (GA); Jekyll Island, edge of sand dunes, 23 Oct 2001, *McNeilus 01-365* (LSU); Sea Island, E of Cloisters Hotel, sandy soil, 28 Nov 1935, *Pyron & McVaugh 195* (GA); Jekyll Island, along E side of South Beach Drive opposite 4-H soccer fields, 3.3 km S of intersection with causeway (Jekyll Island Rd/Ga Hwy 520), 21 Sep 2003, *Thom & Weng 219* (GA). Long Co.: 5.8 mi W of Hwy 301 on Ga Hwy 261, turkey oak, sandy slope, 6 Oct 1962, *Bozeman 1903* (NCU); Griffin Ridge WMA, 1st entrance off Hwy 301S, sandhills, 12 Sep 1999, *Holland 218* (GA). McIntosh Co.: Sapelo Island, 3 mi due N of S end and on inland side, open pine-live oak woods, 15 Oct 1956, *Duncan 20655* (BRIT, GA, SMU, TEX, VSC); 3.0 mi W of Darien, dry sandy bluff, 17 Sep 1961, *Harmer 1356* (GA). **Bahamas**. Grand Bahama: Bootle Bay Village area, old field, large colonies to 1 m high, 8 Nov 1973, *Correll 40678* (LL, TEX); Freeport, intersect. of Settlers Way and East Mall, burnt-over pineland, 14 Aug 1974, *Correll & Kral 42822* (VDB). **Belize**. Toledo District: Near Jenkins Creek, open pine ridge, 26 Aug 1942, *Gentle 4091* (LL).

The collection cited here for *Pityopsis tracyi* in Belize is in a distantly disjunct locality for the species and perhaps could be an aberrant plant of *P. graminifolia* (see Map 1), but it appears to differ morphologically from other *P. graminifolia* in Mexico and Central America. Typical *P. graminifolia* has been collected in the El Cayo District of Belize (e.g., *Hunt 7*, LL; *Lundell 6630*, LL, TEX).

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PEDICULARIS RIGGINSIAE (OROBANCHACEAE), A NEW SPECIES FROM AN AREA OF BOTANICAL ENDEMISM IN CENTRAL-COASTAL CALIFORNIA

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ABSTRACT

Pedicularis rigginsiae D.J. Keil (Orobanchaceae) is a described as a new species from the Arroyo de la Cruz area of northwestern San Luis Obispo Co., California, where it occurs with several other localized endemic taxa. It is distinguished from *P. densiflora* by its smaller stature and leaves, much smaller flowers, and pink rather than red or maroon corolla. It differs from *P. dudleyi*, with which it was initially confused, by its narrower leaves with more numerous lateral lobes, straight rather than distally bent galea, and shorter lower corolla lip. It grows in dwarfed maritime chaparral on windswept coastal terraces east of Highway 1.

The publication of *The Vascular Plants of San Luis Obispo County, California* (Hoover 1970) established a base line for botanical studies of the flora of this diverse county. In the intervening years additional taxa have been documented from the county, many representing extensions of the known ranges of native taxa, some regrettably the spread of invasive species, and a few the discovery of taxa new to science. Accompanying this have been revolutions in understanding of phylogenetic relationships, numerous reclassifications and name changes, and a proliferation of electronic resources. These new advances allow more efficient understanding of novel biodiversity. The need for an update of the county flora has long been evident, and I am nearing completion of a revised edition (Keil & Hoover, in prep.). One of the discoveries resulting from this research is the subject of this paper.

A population of a *Pedicularis* (then Scrophulariaceae, now Orobanchaceae), representing a species that had not been documented previously from San Luis Obispo County, was discovered during a series of field trips in the 1980s to the areas near Arroyo de la Cruz on the Hearst Ranch in the northwestern corner of the county. This area is well known for the presence of rare plants, including several endemics: e.g., *Arctostaphylos cruzensis* Roof, *Arctostaphylos hookeri* G. Don subsp. *hearstiorum* (Hoover & Roof) P. Wells, *Bloomeria humilis* Hoover, *Ceanothus maritimus* Hoover, and *C. hearstiorum* Hoover & Roof (Keil & McLeod 1987; Keil 1997). Hoover (1970) described the area as the "Cruzian pocket of endemism," a subset of his Lucian Endemism Area. Based on a 1981 determination by L.R. Heckard of a specimen of this *Pedicularis* (*Riggins 1208*, JEPS82365), Riggins (1983) reported the newly discovered *Pedicularis* as *P. dudleyi* Elmer, a species otherwise known from southern San Mateo County to northern Monterey County, with its southernmost population about 80 km to the northwest of the Arroyo de la Cruz site. Vorobik (1993, 2012), while treating the Arroyo de la Cruz plants under *P. dudleyi*, suggested that they warranted further study and noted differences from their northern relatives. After further investigation I have determined that the Arroyo de la Cruz plants are not *P. dudleyi* and describe them here as a new species, *Pedicularis rigginsiae*, Arroyo de la Cruz lousewort, thus recognizing yet another endemic from the Arroyo de la Cruz area.

PEDICULARIS RIGGINSIAE D.J. Keil, **sp. nov.** (Figs. 1–3). **TYPE: CALIFORNIA.** San Luis Obispo Co.: Mesa S of Arroyo de la Cruz, 1 mi. E of Highway 1, 11.6 mi. N of San Simeon; common where *Arctostaphylos hookeri* subsp. *hearstiorum* grows, ca. 100 m, [35.707°, –121.285°], 11 Apr 1981, *R. Riggins 1208* (holotype: OBI100071 (Fig. 2); isotypes, JEPS82365 + others to be distributed).

Plant 6–30 cm from a stout, sometimes branched root crown. Stems glabrous or short-villous with soft, multicellular hairs. Foliage leaves deep red to green, petioled, mostly basal, the largest, 8–14 cm, blade 1.5–4 cm wide, narrowly elliptic, pinnately divided into (14) 28–38 linear to triangular-ovate lobes, the larger lobes shallowly lobed and sharply dentate or doubly dentate, distalmost lobes reduced to teeth, petioles glabrous or sparsely villous, both blade faces glabrous. Inflorescence a spike, 2–10 cm; bracts reddish green, 9–15 (25) mm, proximally widest, pinnately lobed and sharply toothed, distally dentate or serrate. Calyx 6–9 mm, short-villous with soft multicellular hairs, minutely glandular-puberulent, lobes 5, ± equal; corolla 13–23 mm, club-like, glabrous, tube included in calyx, tube-galea transition indistinct, upper lip forming a hooded, straight galea, 11–13 mm, open in distal 6–9 mm, pink or distally rose-purple, lower corolla lip 2–3.5 mm, white, middle lobe narrower and slightly longer than laterals; anthers 1.7–2.2 mm, anther sac bases acute. Capsule 6–7 mm, ovoid; seeds 2–3 mm, surface netted. Chromosome number: $n = 8$.

Paratypes. San Luis Obispo Co.: Mesa S of Arroyo de la Cruz, 1 mi E of Hwy 1, 11.6 mi N of San Simeon, common where *Arctostaphylos hookeri* subsp. *hearstiorum* grows, ca. 100 m, [35.707°, –121.285°], 16 Mar 1980, *Riggins 1195* (JEPS82364); ca. 1 mi E of California Rte. 1 on Hearst Ranch, wind-swept coastal hills and canyon area, most shrubs on windward slopes severely wind-pruned forming prostrate mats or a dwarf shrubland, soil heavily compacted, recently moist, scattered among prostrate branches of *Arctostaphylos hearstiorum* on windswept hilltop, 18 May 1980, *Keil 14011* with McLeod, Luckow, Vanderwier, et al. (OBI100073); N of San Simeon in vicinity of Arroyo de la Cruz, along ridge system just S of the arroyo, windswept coastal hills with severely wind-pruned shrubs and trees, local in low-growing chaparral shrubs, galea pink, 30 Jan 1982, *Keil 15678* with Roberts and Raiche (OBI100072); between Cinnabar Hill and Oak Knoll, S of Arroyo de la Cruz, windswept patch of dwarf maritime chaparral, apparently hemiparasitic on *Adenostoma fasciculatum*, 11 Feb 2002, *Keil 29742* with Cox, Sage, and Sage (OBI100074); Santa Lucia Mountains, Arroyo de la Cruz, Cinnabar Hill, mixed chaparral, probably on *Adenostoma*, w/*Ceanothus hearstiorum*, *C. maritimus*, *Arctostaphylos cruzensis*, *A. hearstiorum*, *A. tomentosa*, 155 m, 35.7141°, –121.2797°, 16 Mar 1985, *Hrusa, Griffiths, & Ragan 3600* (CDA20789).

During the study of this species, several specimens of *Pedicularis rigginsiae* were sent to a collaborator who failed to return all of the loaned specimens. At this point these specimens are considered to be missing. These included a specimen I had originally annotated as the holotype of the new species (*Riggins 1208*, OBI80783) plus several annotated as paratypes (*Riggins 1195*, OBI80782; *Keil et al. 14011*, OBI75134; *Keil et al. 15678*, OBI32234; *Keil and Meridith 18124*, OBI45429). The specimen here designated as the holotype (*Riggins 1208*, OBI100071, Fig. 2) is a duplicate of the specimen I originally annotated as holotype; if the latter is rediscovered it must be considered an isotype. Three of these specimens (*Riggins 1195*, OBI80782; *Keil et al. 14011*, OBI75134; *Keil et al. 15678*, OBI32234) are duplicates of specimens cited above as paratypes, and if rediscovered they should be treated as paratypes as well. The last missing specimen, if rediscovered, should also be treated as a paratype: San Luis Obispo Co.: Ridge system S of Arroyo de la Cruz; windswept coastal hills; ridge tops and windward slopes with severely wind-dwarfed shrubs and trees; locally common in fringes of chaparral with chamise and dwarf manzanitas, 14 Apr 1984, *Keil 18124* with Meredith (OBI45429).

Figure 1. Inflorescence of *Pedicularis rigginsiae* (photograph by Rhonda Riggins).

Figure 2. Holotype of *Pedicularis rigginsiae* (*Riggins 1208*, OBI100071).

Figure 3. Habit of *Pedicularis rigginsiae.* Leaves of *Arctostaphylos hookeri* subsp. *hearstiorum*, the putative host, on right. Photo by Rhonda Riggins.

Figure 4. Habitat of *Pedicularis rigginsiae.* Coastal terrace grassland south of Arroyo de la Cruz with mounds of wind-pruned maritime chaparral and coastal live oak woodland in background. Large grass-like clumps are *Carex obispoensis*. Photo by David Keil.

Etymology and common name. The specific epithet honors Dr. Rhonda Riggins, Professor Emeritus at California Polytechnic State University, San Luis Obispo, and student of annual *Lupinus*, who first reported the Arroyo de la Cruz lousewort. I recommend "Arroyo de la Cruz lousewort" as the common name for *Pedicularis rigginsiae*.

Location and ecology. The Arroyo de la Cruz endemic area is in the northwestern part of San Luis Obispo County in the central-coastal part of California, situated between the shoreline and the Santa Lucia Range north of San Simeon. The part of the endemic area to the west of Highway 1 was transferred to state ownership in 2005, but the Hearst Corporation retained possession of the area east of the highway where *Pedicularis rigginsiae* grows. The Hearst Ranch portion of the endemic area is part of an active cattle ranch with a conservation easement in place. Public access is restricted by the Hearst Corporation. To date the only documented occurrences of *P. rigginsiae* are from an area directly to the south of Arroyo de la Cruz and about a mile east of Highway 1, but nearby areas of similar habitat have not been thoroughly explored.

Topography of the Arroyo de la Cruz endemic area is a stairstep-like series of Pleistocene coastal terraces. Flat-topped or gently sloping terrace surfaces have been dissected by coastal stream-courses, arroyos, and gullies. Soils on the terraces are clay-rich, at least in part derived from highly weathered ultramafic parent materials. Coarser substrates are exposed on steeper slopes and on eroded surfaces. Salt-bearing northwesterly coastal winds sweep across the terraces, and trees and shrubs in exposed areas are generally dwarfed and wind-pruned, sometimes to only a few cm above the ground. In a memorable scene from one of the windswept terraces, I observed flowers of *Calochortus albus* (fairy lantern) hanging above the prostrate canopy of a mature *Quercus agrifolia* (coast live oak)! Grasslands occupy much of the exposed terraces, with a diversity of annual and perennial wildflowers growing among native and Mediterranean grasses. Although some terrace areas were cultivated fields in the past and consequently have a high proportion of introduced species, large areas have never been plowed and support a rich native flora. Interfingering with the grasslands are areas of dwarfed maritime chaparral (Fig. 4) that include endemic or near-endemic shrubs such as *Arctostaphylos cruzensis*, *A. hookeri* subsp. *hearstiorum*, *Ceanothus maritimus*, and *C. hearstiorum*, and more widespread taxa such as *Arctostaphylos tomentosa* subsp. *tomentosa* and *Adenostoma fasciculatum*. *Ceanothus maritimus* extends into the grasslands in places as a prostrate shrubby understory beneath the grasses. It is within the dwarf chaparral and its ecotone with grasslands that *Pedicularis rigginsiae* occurs. I suspect, based on observed associations, that *P. rigginsiae* establishes root connections with both *Arctostaphylos hookeri* subsp. *hearstiorum* and *Adenostoma fasciculatum*, but attachments to the putative hosts have not been documented.

Relationships. Two other species of *Pedicularis* occur in California's South Coast Ranges: *P. dudleyi* and *P. densiflora* Hook. Phylogenetic analyses by Robart et al. (2015) indicate that *P. dudleyi* and *P. densiflora* are closely related, and the two appear as sister taxa in their phylogenies.

Monfils and Prather (2007) distinguished *Pedicularis aurantiaca* (E.F. Sprague) Monfils & Prather as a close relative of *P. densiflora* that occurs in the Sierra Nevada, Cascade, and eastern Klamath Ranges, but not in the western Klamath and Coast Ranges where *P. densiflora* grows. Robart et al. (2015) did not include *P. aurantiaca* in their analyses; their DNA source for *P. densiflora* was a specimen collected in Marin County in the North Coast Range. Vorobik (2012) did not treat *P. aurantiaca* in her Jepson Manual treatment of *Pedicularis*, but synonymized its basionym, *P. densiflora* subsp. *aurantiaca* E.F. Sprague in the 1993 edition of the manual.

Chuang and Heckard (1992) indicate that most *Pedicularis* species are diploids with $n = 8$. Keil in Riggins (1983) reported a chromosome count of $n = 8$ for *P. rigginsiae* [as *P. dudleyi*]. Spellenberg (1971), Carr (1972), and Chuang and Heckard (1992) reported counts of $n = 8$ for *P. densiflora* from Trinity, Napa, and Marin counties, respectively. Chuang and Heckard's chromosome voucher is a duplicate of the specimen from which Robart et al. (2015) obtained their DNA sample for *P. densiflora*. Carr (1972) reported a count of $n = 8$ for a San Mateo County population of *P. dudleyi*. No counts have been reported for *P. aurantiaca*.

Table 1. Comparison of features of *Pedicularis* species in California's South Coast Range.

	Pedicularis rigginsiae	***Pedicularis dudleyi***	***Pedicularis densiflora***
Stature	6–30 cm	10–20 cm	6–55 cm
Vestiture	Stems glabrous or villous; leaves glabrous; bracts glabrous; calyx minutely villous	Stems villous; leaves glabrous or villous on one or both faces; bracts abaxially villous; calyx villous	Stems glabrous to densely villous; leaves abaxially glabrous, puberulent, or villous, adaxially glabrous; bracts glabrous or margins and abaxial face villous; calyx glabrous or villous
Length of largest leaf	8–14 cm	15–25 cm	10–30 cm
Width of largest leaf blade	1.5–4 cm	4–6 cm	4–8(15) cm
Number of lateral lobes of largest leaves (distalmost reduced to teeth)	(14) 28–38	12–24	20–36
Inflorescence length	2–10 cm	2–5 cm	4–20+ cm
Bract characteristics	9–15 mm, proximally widest, pinnately lobed and sharply toothed, distally dentate or serrate	12–27 mm, proximally narrowed to a sometimes petiole-like base, distally sharply serrate	(10) 20–50 mm, proximally narrowed to petiole or ± entire, petiole-like base, distally ± expanded, sharply toothed or lobed; proximal-most flowers sometimes in axils of unmodified distal foliage leaves
Calyx length	6–9 mm	10–11 mm	8–15 mm
Corolla color	white to pink, sometimes aging rose-purple	pink	red or maroon (yellow or purple)
Corolla length	13–23 mm	17–18 mm	23–36 mm
Galea	8–13 mm, straight	10–11 mm, distally down-curved	8–17 mm, straight
Lower corolla lip	2–3.5 mm	6 mm	8–12 mm
Capsule length	6–7 mm	± 12 mm	8–13 mm
Seed length	2–3 mm	not available	2.5–4.5 mm

Pedicularis rigginsiae is easily distinguishable from *P. dudleyi* and *P. densiflora* by the characteristics delineated in Table 1. Monfils and Prather (2007) made a detailed comparison of *P. aurantiaca* and *P. densiflora* and illustrated characteristics of the two taxa. The four species may be separated using the following key.

1. Corolla 13–23 mm, white to pink (sometimes aging rose-purple).
    2. Leaves 1.5–4 cm wide; galea straight; lower corolla lip 2–3 mm, lobes unequal, the lateral rounded ..... **Pedicularis rigginsiae**
    2. Leaves 4–6 cm wide; galea distally down-curved; lower corolla lip ± 6 mm, lobes ± equal, all acute ..... **Pedicularis dudleyi**

1. Corolla 23–43 mm, usually red or maroon (yellow, orange, or purple).
    3. Calyx 12–24 mm; lower corolla lip < 8 mm; galea opening > 4/5 its length; corolla tube included within calyx lobes at time of flowering ..... **Pedicularis aurantiaca**
    3. Calyx 10–18 mm; lower corolla lip ≥ 8 mm; galea opening < 4/5 its length; corolla tube exserted beyond calyx lobes at time of flowering ..... **Pedicularis densiflora**

Rarity Status. I recommend to the California Native Plant Society that *Pedicularis rigginsiae* be included in the *Inventory of Rare and Endangered Plants of California* with a California Rare Plant Rank of 1B.1—Rare and Endangered in California and Elsewhere. Although the area of the Hearst Ranch where *P. rigginsiae* occurs is under a conservation easement and the ranch has been conservatively managed, the facts that the site is part of an active cattle ranch and that the species has just one known occurrence justify a Threat Rank of 0.1—Seriously threatened in California (over 80% of occurrences threatened/high degree and immediacy of threat). When evaluated using IUCN (2000) Red List criteria, *P. rigginsiae* qualifies as Endangered (EN) – High risk of extinction in the wild, based on extent of occurrence estimated to be less than ~100 km^2. The recognition of the Arroyo de la Cruz lousewort as a distinct species decreases the known range of *P. dudleyi*. *Pedicularis dudleyi* has a California Rare Plant Rank of 1B.2 (CNPS Rare Plant Program 2015), and I recommend that it retain that status.

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NEW VARIETAL COMBINATIONS IN *DIPLACUS* FOR THE SHRUBBY MONKEYFLOWERS, THE *DIPLACUS AURANTIACUS* COMPLEX (PHRYMACEAE)

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ABSTRACT

New combinations are made at the varietal level within *Diplacus aurantiacus* (Phrymaceae) for eight taxa previously treated at the species level in *Diplacus* and/or at the varietal level in *Mimulus*: **Diplacus aurantiacus** (Curtis) Jeps. var. **aridus** (Abrams) D.J. Keil, **comb. nov.**; **Diplacus aurantiacus** (Curtis) Jeps. var. **calycinus** (Eastw.) D.J. Keil, **comb. nov.**; **Diplacus aurantiacus** (Curtis) Jeps. var. **grandiflorus** (Lindl. & Paxton) D.J. Keil, **comb. nov.**; **Diplacus aurantiacus** (Curtis) Jeps. var. **linearis** (Benth.) D.J. Keil, **comb. nov.**; **Diplacus aurantiacus** (Curtis) Jeps. var. **×lompocensis** (Munz) D.J. Keil, **comb. nov.**; **Diplacus aurantiacus** (Curtis) Jeps. var. **longiflorus** (Nutt.) D.J. Keil, **comb. nov.**; **Diplacus aurantiacus** (Curtis) Jeps. var. **parviflorus** (Greene) D.J. Keil, **comb. nov.**; and **Diplacus aurantiacus** (Curtis) Jeps. var. **puniceus** (Nutt.) D.J. Keil, **comb. nov.** Lectotypes are designated for *Diplacus calycinus* Eastw., *Mimulus linearis* Benth., *Diplacus longiflorus* Nutt., and *Diplacus puniceus* Nutt.

The bush monkeyflowers are prominent, showy, and often common components of various widespread plant communities in California and the adjacent regions of southwestern Oregon and northwestern Baja California that together form the California Floristic Province. Although displaying considerable similarity in vegetative form, with some variation in leaf shape and pubescence, these plants show diversity in floral form and color. Since the introduction of bush monkeyflowers to European gardens in the late 1700s, taxonomists have proposed many names to account for the variation. During the past century taxonomists have attempted to bring order to these plants in floras and in more focused studies, but to date there is not a consensus about how to classify them.

Thompson (2005) published a monograph of subg. *Schizoplacus* A.L. Grant of what was at the time treated as the large genus *Mimulus* L., then placed in Scrophulariaceae. He had previously treated *Mimulus* for *The Jepson Manual* (Thompson 1993). The cohesiveness of the Scrophulariaceae was already in question (Olmstead et al. 2001), and the placement of *Mimulus* into a redefined Phrymaceae soon followed (Beardsley & Olmstead 2002). Beardsley and Barker (2005) provided evidence that *Mimulus* (sensu lato) is not monophyletic. Barker et al. (2012) presented a revised generic conspectus of Phrymaceae in which *Mimulus* was broken apart, and the plants that Thompson had treated as *Mimulus* subg. *Schizoplacus* were reassigned to a resurrected and expanded genus *Diplacus* Nutt.

The shrubby monkeyflowers, which Thompson (2005) treated as *Mimulus* sect. *Diplacus*, have been variously classified in past studies. Some authors have recognized them as the genus *Diplacus* along with an herbaceous relative, *D. clevelandii* (Brandegee) Greene. Jepson (1925) recognized *Diplacus* with six species in California, and McMinn (1939) recognized seven species. In his revision of *Diplacus* (McMinn 1951b) and in the second edition of his *Illustrated Manual of California Shrubs* (McMinn 1951a), McMinn accepted *Diplacus* as a genus of 14 species and

stabilized hybrids including the herbaceous *D. clevelandii* and acknowledged a plethora of additional natural and artificial hybrids. However, he noted this:

> I have chosen to treat all these field entities (taxa) simply as binomials. Inasmuch as binomials to most botanists indicate species, I have endeavored not to use the word species when writing of these various entities. I must point out, however, that if sterility and geographical distribution tests were the main criteria applied in delimiting species and subspecies, then the field entities of the genus *Diplacus* probably would be classified as two taxonomic species [*D. aurantiacus* and *D. clevelandii*], eleven subspecies, and numerous hybrids.

Other botanists have retained the shrubby monkeyflowers within *Mimulus*. Grant (1924) recognized 8 species in *Mimulus* sect. *Diplacus* (Nutt.) Benth. & Hook.f. plus three additional varieties. Abrams (1951) also treated them in *Mimulus* sect. *Diplacus*, recognizing eight species in California (including *M. clevelandii* Brandegee) plus two subspecies. Munz (1959) also placed these species in *Mimulus* and dealt with the variability by recognizing six species plus five additional infraspecific taxa. Thompson (1993) placed all of the California species of sect. *Diplacus* except *M. clevelandii* into synonymy under *M. aurantiacus* Curtis, acknowledging these plants to be "highly complex, with many intergrading, hybridizing, local forms." Thompson (2005), attempting to sort the variation into geographical races, recognized six varieties of *M. aurantiacus* while acknowledging that "hybridization occurs wherever any two varieties come together" and that "a large proportion of specimens are intermediate to some degree and some of these may not easily key to a recognized variety." Thompson was not the first to act on the proposition that these plants were perhaps better treated as a single highly variable species. Over 150 years earlier Lindley and Paxton (1852), noting the extreme variability of the members of the complex known to them, recognized four varieties of what was then called *Diplacus glutinosus* Nutt.

Tulig and Nesom (2012) accepted the disintegration of *Mimulus* (sensu lato) and treated the shrubby monkeyflowers plus *Diplacus clevelandii* as *Diplacus* sect. *Diplacus*. They recognized thirteen taxa, all at the species rank, including the Cedros Island endemic *D. stellatus*, and hypothesized three of these to be nothospecies: *D.* ×*australis* (McMinn ex Munz) Tulig [putatively *D. longiflorus* Nutt. × *D. puniceus* Nutt.], *D.* ×*linearis* (Benth.) Greene [putatively *D. calycinus* Eastw. × *D. aurantiacus* (Curtis) Jeps.], and *D.* ×*lompocensis* McMinn [putatively *D. aurantiacus* × *D. longiflorus* Nutt.]. Nesom (2013) backed away from the idea that *D. linearis* is of hybrid origin. Although they hypothesized three taxa as nothospecies, Tulig and Nesom downplayed hybridization in advocating for recognizing multiple species: "Each of the taxa of sect. *Diplacus* has a distinct geographic range and for the most part is clearly defined (Fig. 4), and throughout most of the range of sect. *Diplacus*, hybridization appears to be limited."

Stankowsky and Streisfeld (2015) and Chase et al. (2017) investigated the relationships of the taxa comprising *Mimulus* sect. *Diplacus* using a variety of methods including phylogenetic analyses of genomewide single nucleotide polymorphism data, population genomic analyses, tests for hybridization, and multivariate analyses of floral trait data. Chase et al. (2017) compared the classification hypotheses presented by Thompson (2012), Tulig and Nesom (2012), and earlier investigators in terms of the results of their analyses. The Chase et al. (2017) study included all of the taxa recognized as varieties of *M. aurantiacus* by Thompson and all recognized as species or nothospecies in *Diplacus* by Tulig and Nesom except the insular *D. stellatus*. Phylogenetic analyses identified four highly supported primary clades within the bush monkeyflowers plus the herbaceous *M. clevelandii* as their sister group. Chase et al. found evidence for recent gene flow between closely related subclades and populations and discordance between floral trait characters and molecular data that provides evidence for divergent and convergent phenotypic evolution. The taxonomies of both Thompson (2012) and Tulig and Nesom (2012) were reflected in the phylogenetic analyses with some exceptions. *Diplacus australis, D. rutilus* (A.L. Grant) McMinn, and *D. calycinus*, all recognized by

Tulig and Nesom appear in the analyses to be polyphyletic. Southern California plants treated by Thompson as *M. aurantiacus* var. *aurantiacus* (and by Tulig and Nesom as *D.* ×*australis*) were phylogenetically isolated from the remainder of *M. aurantiacus*. The hypotheses by Tulig and Nesom that two species, *D. linearis* and *D. australis*, were of hybrid origin were not supported by other analyses in the Chase et al (2017) study. Instead *D. linearis* was resolved as a monophyletic sister group of *D. grandiflorus,* and samples of *D. australis* were interdigitated among samples of *D. puniceus*, with no indication of hybridization involving *D. longiflorus.* Two samples of *D. calycinus* were phylogenetically isolated from the remaining samples of that species. Additional analyses in the Chase et al. study indicate that these two samples are probably of hybrid origin.

In her treatment of Phrymaceae for the Jepson eFlora, Fraga (2018), although aware of the Chase et al (2017) study, chose to treat the various shrubby monkeyflowers at the species level. Fraga (pers. comm.) believes that contrary to the conclusions of its authors "the Chase et al. paper provides evidence for recognition of several taxa as species." In her treatment Fraga recognized nine California species: *Diplacus aridus*, *D. aurantiacus*, *D. australis*, *D. calycinus*, *D. grandiflorus*, *D. linearis*, *D. longiflorus*, *D. parviflorus*, and *D. puniceus*. In contrast to Tulig and Nesom, she treated *D. australis* and *D. linearis* as full species, but agreed with them that *D.* ×*lompocensis* is a hybrid between *D. aurantiacus* and *D. longiflorus*. She did not comment on the results of the Chase et al. study that indicated *D. australis* is polyphyletic.

Though the overall outline of relationships in the shrubby monkeyflowers has been established, it remains necessary to ask the question of taxonomic rank for the various morphotypes. Chase et al. (2017) addressed this issue, first by quoting the same passage from McMinn (1951) that is presented above and then directly addressing the issue:

> In most of the previous treatments of this group, the rank employed appears arbitrary and often was not justified by the authors. However, given the interfertility, natural hybridization, and shared genomic variation present among taxa, we support the view by McMinn (1951), and more recently by Thompson (2012), who treated the taxa (with the exception of *M. clevelandii*) as intraspecific subspecies or varieties of *M. aurantiacus.* This view, which acknowledges the reproductive continuity and close relationships among these taxa, emphasizes our need to understand how and why so much diversity arose and has been maintained within this group.

I agree with Chase et al. that treating the shrubby monkeyflowers as variants of a single species is to be preferred. Over my career as a field botanist and herbarium curator in California, I've attempted to use both the multispecies approach, especially as applied by Munz (1959) and Hoover (1970), and Thompson's (1993, 2012) *Jepson Manual* treatments of the variants as part of a single species, and I much prefer the latter. I view these plants as a partially differentiated assemblage of races that have not reached the level of stability that is usually associated with the concept of species. Certainly there is much variation within the group that deserves a level of taxonomic recognition, or at least should be mentioned, but I think it more prudent to recognize varieties—entities that may be expected to freely intergrade—than species. From a practical standpoint as a curator, I know that using a multispecies taxonomy results in forcing many specimens into inappropriate pigeonholes plus a large number of intermediate specimens unassignable to species and not readily fileable.

I'm nearing completion of the second edition of the Vascular Plants of San Luis Obispo County, California (Keil & Hoover in prep.), and I want to treat the shrubby monkeyflowers with nomenclature that is both up to date and practical. I welcomed Thompson's taxonomic approach as a realistic acknowledgement of the complex patterns of variation in these plants, but I accept the breakup of the monkeyflowers into segregate genera. The authors of the Chase et al. 2017 paper have communicated that they do not plan to propose any nomenclatural changes based on their research (Streisfeld, pers. comm.). Therefore I propose new combinations at the varietal level in *Diplacus aurantiacus* to accommodate the taxa that form this wonderful example of evolution in progress. I

use the varietal rank rather than subspecies because this is the rank that has been applied in most past studies in this group that recognized infraspecific taxa. Most plant taxonomists treat these ranks as taxonomically interchangeable, though nomenclaturally they are not.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **ARIDUS** (Abrams) D.J. Keil, **comb. nov.** *Diplacus aridus* Abrams, Bull. Torrey Bot. Club 32: 540. 1905. *Mimulus aridus* (Abrams) A.L. Grant, Ann. Missouri Bot. Gard. 11: 336. 1925. *Mimulus aurantiacus* Curtis var. *aridus* (Abrams) D.M. Thomps., Syst. Bot. Monogr. 75: 158. 2005. **TYPE**: **USA. California.** San Diego Co.: "Jacumba, near the [U.S.A. boundary] monument," 31 May 1903, *L. Abrams 3656* (holotype: NY 68331, image!); isotypes: BM, CAS, E, GH2, K, MO, PH-2, POM, RSA, UC-2, US).

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **CALYCINUS** (Eastw.) D.J. Keil, **comb nov.** *Diplacus calycinus* Eastw., Bot. Gaz. (Crawfordsville) 41: 287. 1906. *Mimulus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey var. *calycinus* (Eastw.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 331. 1924. *Diplacus longiflorus* Nutt. var. *calycinus* (Eastw.) Jeps., Man. Fl. Pl. Calif. 919. 1925. *Mimulus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey subsp. *calycinus* (Eastw.) Munz, Aliso 4: 99. 1958. **LECTOTYPE** (here designated): **USA. California**. Tulare Co.: "So. Fork Kaweah River, 6000 ft," 22 Jul 1904, *Culbertson s.n.* (*C.F. Baker 4407*) (CAS 28303, image!; isolectotypes: CAS, GH, K, MO, NY, PH, POM, UC).

Eastwood (1906) cited the type collection of *Diplacus calycinus* as follows: "The type is 4407 of C. K. Baker's distribution, collected by Culbertson in the south fork of Kaweah River, 1800^{m} altitude, July 22, 1904." Thompson (2005) cited CAS 28303 as the holotype of *Diplacus calycinus*. However, Eastwood did not designate the herbarium in which the specimen(s) she examined were deposited. According to ICN Art. 40, Note 1 (Turland et al 2018), because there are duplicates of this collection, the specimen(s) Eastwood examined and the duplicates are to be treated as synytpes. Had Thompson made this error prior to 1 Jan 2001 this designation would have been a correctable error (ICN Art. 7.11, Ex. 13; 9.10) with Thompson's citation of CAS 28303 as holotype correctable to lectotype (sometimes described as inadvertent lectotypification (Prado et al. 2015)). However, ICN Art. 7.11 and 9.23 require that on or after 1 Jan 2001 designation of lectotype must be specifically indicated. I therefore am designating CAS 28303 as lectotype of *D. calycinus*.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **GRANDIFLORUS** (Lindl. & Paxton) D.J. Keil, **comb. nov.** *Diplacus glutinosus* (J.C. Wendl.) Nutt. var. *grandiflorus* Lindl. & Paxton, Paxt. Fl. Gard. 3: 96, plate 92. 1852. *Mimulus aurantiacus* var. *grandiflorus* (Lindl. & Paxton) D.M. Thompson, Monogr. Syst. Bot. 75: 158. 2005. **NEOTYPE** (Thompson 2005): **USA. California.** Butte Co.: "Between Chico and Forest Ranch, elev. 2000 ft," 18 May 1914, *A.A. Heller 11407* (UC 196052); isoneotypes: A, CAS, CU, DS, E, F, GH, MO, ND-G, NY, OSC, PENN, PH-2).

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **LINEARIS** (Benth.) D.J. Keil, **comb. nov.** *Mimulus linearis* Benth, Scroph. Ind. 27. 1835. *Mimulus glutinosus* J.C. Wendl. var. *linearis* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876. *Diplacus linearis* (Benth.) Greene, Pittonia 2: 156. 1890. *Mimulus glutinosus* J.C. Wendl. forma *linearis* (Benth.) Voss in Vilmorin, Vilm. Blumengartn. (ed. 3) 1: 762. 1895. *Mimulus longiflorus* Nutt. var. *linearis* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 334. 1924. *Diplacus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey var. *linearis* (Benth.) McMinn, Man. Calif. shrubs (ed. 1) 498. 1939. **LECTOTYPE** (here designated): **USA. California.** Without locality, 1833, *D. Douglas s.n.* (K-herb. Bentham (K 001079320, image!); isolectotypes: BM, E, GH, K-herb. Hooker, NY, OXF).

As in the situation described above for *Diplacus calycinus*, Thompson's (2005) citation of the Douglas collection in Bentham's herbarium (K001079320) as holotype of *Mimulus linearis* is

incorrect, as there are several duplicates deposited in other herbaria. I therefore am designating K 001079320 as lectotype of *M. linearis*.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. ×**LOMPOCENSIS** (Munz) D.J. Keil, **comb. nov.** — *Diplacus lompocensis* McMinn, Madroño 11: 62. 1951. *Mimulus aurantiacus* Curtis subsp. *lompocensis* (McMinn) Munz, Aliso 4: 99. 1958. **TYPE**: **USA. California.** Santa Barbara Co.: "Along Highway [1] between Lompoc and Las Cruces, Santa Inez [Ynez] Mountains," 7 Jun 1949, *H. McMinn 5601* (holotype: UC 914709, image!).

Diplacus aurantiacus var. ×*lompocensis* has been hypothesized by various authors (e.g., McMinn 1951, Thompson 2005, Tulig and Nesom 2012) to be a [stabilized?] hybrid between *D. aurantiacus* and *D. longiflorus* (*Mimulus aurantiacus* var. *aurantiacus* and *M. a.* var. *pubescens*) that occupies a coastal area in south-central California from southwestern San Luis Obispo Co. to western Santa Barbara Co. Evidence presented by Chase et al. (2017) supports the hypothesis that these plants are of mixed origin. Whether they represent a stabilized hybrid or recurrent recent hybrids needs further investigation. For practical considerations I am choosing to treat them as a nothosubspecies.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **LONGIFLORUS** (Nutt.) D.J. Keil, **comb. nov.** *Diplacus longiflorus* Nutt., Ann. Nat. Hist. 1(2): 139. 1838. *Mimulus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey, Gentes Herbarum 1(3): 136. 1923. **LECTOTYPE** (here designated): **USA. California.** Santa Barbara Co.: St. Barbara [Santa Barbara], "Mr. Whilatz" [± illegible; the collector?], Herb. Nuttall (BM 001025105, image!; isolectotypes: GH, K).

As in the situation described above for *Diplacus calycinus*, Thompson's (2005) citation of the collection in Nuttall's herbarium (BM 001025105) as holotype of *Mimulus linearis* is incorrect, as there are duplicates deposited in other herbaria. I therefore am designating BM 001025105 as lectotype of *D. longiflorus*.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **PARVIFLORUS** (Greene) D.J. Keil, **comb. nov.** *Diplacus parviflorus* Greene, Pittonia 1(1): 36. 1887. *Mimulus parviflorus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 344. 1925 (nom. illeg.). *Mimulus flemingii* Munz, Man. S. Calif. Bot., 477, 601. 1935. *Mimulus aurantiacus* Curtis var. *parviflorus* (Greene) D.M. Thomps., Syst. Bot. Monogr. 75: 157. 2005. **LECTOTYPE** (Thompson 2005): **USA. California.** Santa Barbara Co.: Santa Cruz Island, Jul & Aug, 1886, *E. L. Greene s.n.* (UC 103629, image!; isolectotypes: A, BM, DS, F, MO, ND-G-2, NY-3, PENN, PH, UC-2, US).

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **PUNICEUS** (Nutt.) D.J. Keil, **comb. nov.** *Diplacus puniceus* Nutt., Ann. Nat. Hist. 1: 137. 1838. *Mimulus puniceus* (Nutt.) Steud., Nomencl. Bot. (ed. 2) 2: 150. 1841. *Diplacus glutinosus* (J.C. Wendl.) Nutt. var. *puniceus* (Nutt.) Benth. in DC., Prodr. 10: 368. 1846. *Mimulus glutinosus* J.C. Wendl. var. *puniceus* (Nutt.) A. Gray, Bot. California 1: 566. 1876. *Mimulus aurantiacus* Curtis var. *puniceus* (Nutt.) D.M. Thompson, Syst. Bot. Monogr. 75: 156. 2005. **LECTOTYPE** (here designated): **USA. California.** San Diego Co.: St. Diego [San Diego], *T. Nuttall s.n.* (BM 001025107, image!; isolectotypes: K, PH).

As in the situation described above for *Diplacus calycinus*, Thompson's (2005) citation of the collection in Nuttall's herbarium (BM 001025107) as holotype of *Diplacus puniceus* is incorrect, as there are duplicates deposited in other herbaria. I therefore am designating BM 001025107 as lectotype of *D. puniceus*.

I am not proposing varietal names in *Diplacus aurantiacus* for four of the taxa treated as species in *Diplacus* sect. *Diplacus* by Tulig and Nesom (2012). The herbaceous *D. clevelandii* is the

sister taxon to the remainder of the section, and I consider it to be a separate species. Phylogenetic evidence presented by Chase et al. (2017) indicated that red-flowered *Diplacus rutilus* does not form a lineage distinct from yellow-flowered *D. longiflorus* and recommended that it be treated as a color morph of *D. longiflorus*. The little-known *D. stellatus* was not included in the studies by Chase et al. (2017), and its status remains unclear. Thompson (2004) included it in the synonymy of *Mimulus aurantiacus* var. *aurantiacus*.

Diplacus australis presents a conundrum. Tulig and Nesom (2012) hypothesized *D. australis* to be of hybrid origin. As mapped by Tulig and Nesom (2012) these plants have a considerable range in southwestern California and northwestern Baja California, largely sympatric with *D. longiflorus* and *D. puniceus*, the putative parental taxa. However, Chase et al. (2017) found no evidence that *D. australis* is of hybrid origin. Sobel and Streisfeld (2015) presented evidence that the yellow-flowered populations treated by Tulig and Nesom (2012) as *D. australis* are differentiated from red-flowered *D. puniceus* by strong premating barriers. However, in the phylogenetic analyses of Chase et al. (2017), samples from the yellow-flowered *D. australis* are not resolved as a monophyletic lineage, but instead are interdigitated with samples of the red-flowered *D. puniceus*. Thus evidence of one sort suggests that *D. australis* is undergoing incipient speciation, which might be considered justification for recognizing these plants at the infraspecific level, but other evidence indicates that populations identified by this name do not represent a single lineage. The question of taxonomic recognition in the California flora was addressed in the Jepson Manual Contributor's Guide (Baldwin et al. 2004):

> A common feature of all taxonomic concepts recognized by The Jepson Flora Project and the modern systematic community in general is that the taxa being recognized should represent natural, evolutionary lineages. Also, because TJM2 will be used (like TJM) as a definitive resource for assessing plant diversity in California (e.g., for conservation planning by state and federal agencies), we seek to capture within it all biologically meaningful, minimal-rank taxa (e.g., species, subspecies, and varieties) recognized to occur in the California flora.

Do the plants treated as *D. australis* represent a natural lineage? Or are they multiple parallel/convergent lineages? Are they a biologically meaningful taxon? Is their incipient speciation biologically meaningful?

The taxonomic rank of forma has been used in some classification schemes for entities distinguished from other members of their species by one or more noticeable features. Members of a form are not necessarily expected to constitute a clade. If the plants that have been treated as *D. australis* were given taxonomic recognition, forma would seem the appropriate taxonomic rank. However, only subspecies and varieties are recognized in the *Jepson Manual* (Baldwin et al. 2004), and I am not proposing a new combination reducing *D. australis* to the rank of forma. Chase et al. (2017) recommended that "even though no previous description of the red-flowered *M. puniceus* exists that also would include the yellow-flowered *M. australis*, we suggest that future revisions incorporate these genomic and ecological patterns into a description that recognizes this divergence in the form of “ecotypes” of the consistently recognized *M. puniceus*." Although Fraga (2018) has treated *D. australis* as a species, I prefer to accept the informal treatment for these plants proposed by Chase et al.

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DITTRICHIA GRAVEOLENS (ASTERACEAE) IS NATURALIZED AND INVASIVE IN NEW YORK STATE

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ABSTRACT

Dittrichia graveolens (Asteraceae) is known from five populations widely scattered on Staten Island, Richmond Co, New York, indicating that the species is naturalized and well-established in New York City and New York state.

Dittrichia graveolens (L.) Greuter (stinkwort) was first collected in New York State in 1949 by Harold Moldenke and Joe Monachino in Bronx County (*Moldenke 20555* and *Monachino 529*). Monachino collected the species again in Brooklyn, Kings Co., in October 1959 (*Monachino 632*). The species was not collected or documented again in New York state until the present work and was thought to be historical (Weldy et al. 2019; Atha & Boom 2018; USDA NRCS 2018; Werier 2017).

Stinkwort is currently known from five populations on Staten Island, Richmond Co, New York (Figure 1): the one documented here with an herbarium specimen and four others documented by iNaturalist observations made in 2017 and 2018 (Lemon Creek Park, Heather Liljengren, iNaturalist observ. *18212895*; Brookfield Park, Catherine Barron, iNaturalist observ. *17291502*; Silver Lake Park, Catherine Barron, iNaturalist observ. *18439357*; Bridge Creek, Catherine Barron, iNaturalist observ. *8057953*).

Voucher specimen. New York. Richmond Co.: New York City, Staten Island, floodplain of Mill Creek, W of Arthur Kill Rd and E of the Arthur Kill, between Richmond Valley Rd and Bethel Ave. 40.520567, -74.240185 (WGS 84, ±5m), ca 2 m elev., 13 Oct 2018, *Atha et al. 16047* (NY).

The species was not collected or reported in New York state between 1959 and 2017. However, we know the species was in the area because Karl Anderson reported it as "fairly common" along roadsides at Liberty State Park, New Jersey (Anderson 1989). It is not known whether the

Staten Island plants documented here are new introductions or whether the species has been in New York state since 1959 but undetected.

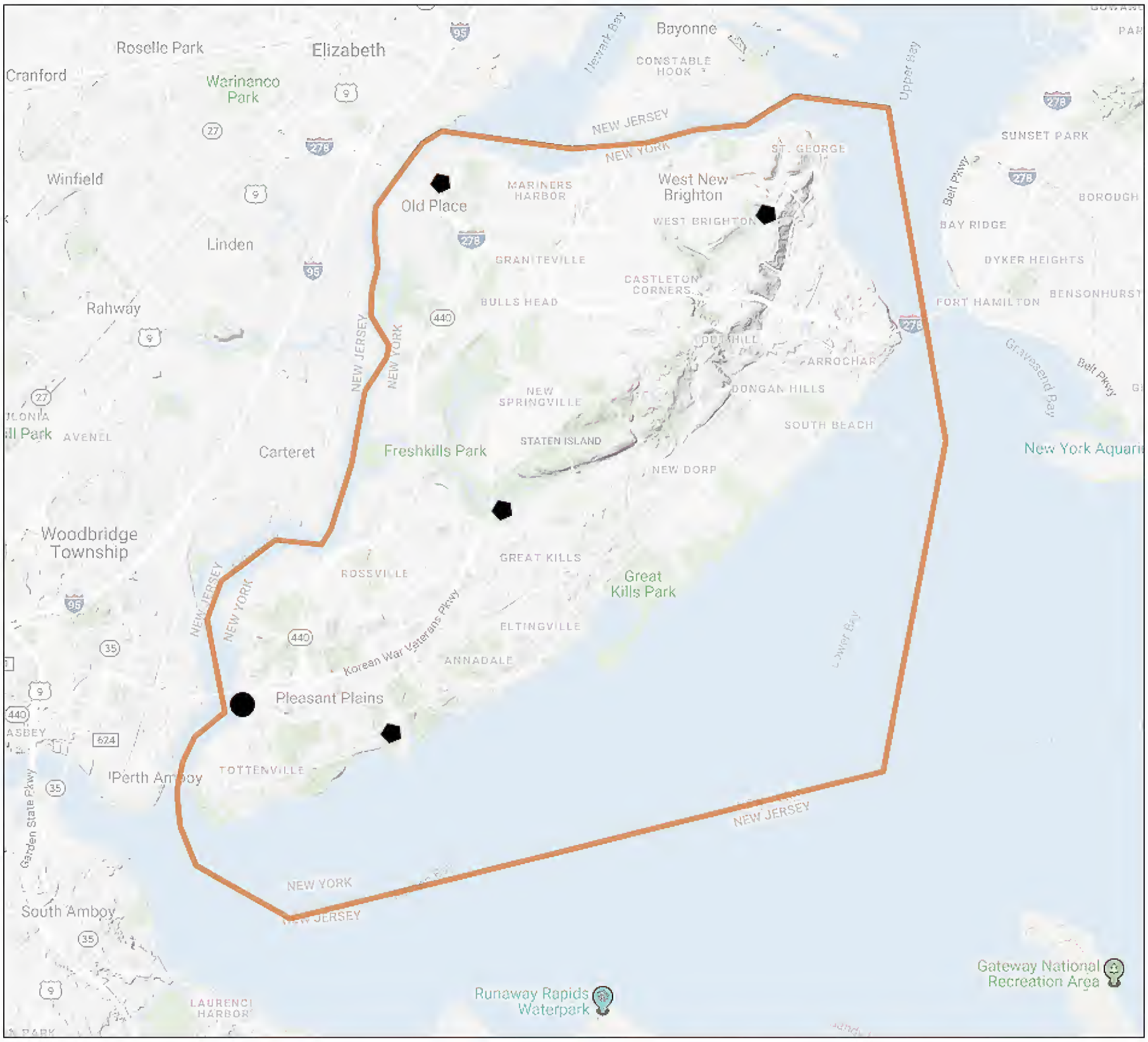

Figure 1. Distribution of *Dittrichia graveolens* on Staten Island, Richmond Co., New York. Polygons are iNaturalist observations and the circle is the herbarium specimen *Atha et al. 16047*. Map adapted from iNaturalist.org.

Dittrichia graveolens is a fall-flowering annual (Fig. 2) native to the Mediterranean region from Spain, Morocco, and North Africa east to southwest Asia through Turkey, Iran, Pakistan and India (Brullo & de Marco 2000). It is the most widespread of the five species in the genus and occurs primarily in anthropogenic habitats such as roadsides, cultivated land, and abandoned fields, especially those high in nitrogen (Brullo & de Marco 2000). The epithet *graveolens* and the common name stinkwort refer to the abundant aromatic glands that occur throughout the plant. The plant contains sesquiterpene lactones which are widespread in the Asteraceae and are known to produce allergic reactions in humans (Preston 1997). Some individuals may exhibit severe dermatological allergic reactions to *Dittrichia graveolens* (Thong et al. 2008).

Figure 2. *Dittrichia graveolens* at 721 Arthur Kill Road, Staten Island, Richmond Co., New York, 7 October 2018 (cbarron, iNaturalist observ. *17291502*).

The species is an aggressive colonizer and in recent years has been spreading rapidly beyond its native range into northern Europe, Australia, and South Africa (Brownsey et al. 2013a; USDA APHIS 2018). It was first detected in Santa Clara Co., California, in 1984 (Preston 1997) and by 2012 had expanded exponentially to 36 counties in the state (Brownsey et al. 2013a). It produces up to 71,000 seeds per plant with a germination rate up to 90% (Brownsey et al. 2013b). Seeds are dispersed by wind, water, animals, and machinery (Brownsey et al. 2013b; USDA APHIS 2018). The seemingly recent and widespread distribution of the plants on Staten Island suggest that they may be spread locally by the movement of contaminated soil, machinery, or both. Researchers at Stanford University's Jasper Ridge Biological Preserve found that cutting and hand-pulling before the plants set seed was nearly 100 percent effective at controlling the species within the preserve (Stanford 2019).

The infestations documented here will be uploaded to the New York State invasive species mapping program iMapInvasives where they will be tracked by city and state authorities including the New York City Department of Parks and Recreation (NYC Parks), Lower Hudson Partnership for Regional Invasive Species Management (LHPRISM), Long Island Invasive Species Management Area (LIISMA) and the New York State Department of Environmental Conservation (NYS DEC). Based on the management success demonstrated at the Jasper Ridge Preserve and because the species currently occurs in isolated populations in low numbers from only one county in the state, we suggest that a rapid response by relevant stakeholders could succeed in eradicating this noxious invasive species from New York State.

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POTENTILLA INDICA (ROSACEAE) NEW TO UTAH, WITH DISCUSSION OF DISPERSAL BY THE AMERICAN ROBIN

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ABSTRACT

Potentilla indica, previously treated under the name *Duchesnea indica*, is first reported here as new to the naturalized flora of Utah (vouchered from urban and suburban habitats in South Ogden, Weber County). The American Robin is discussed as a possible vector of dispersal.

Duchesnea indica (Andrews) Teschem. (Indian strawberry, mock strawberry; Rosaceae) was realigned into *Potentilla* by Eriksson et al. (1998), where its correct name is *Potentilla indica* (Andrews) T. Wolf. *Duchesnea* as a genus is phylogenetically nested within the larger and more widespread genus *Potentilla*. This placement of *Duchesnea* has been supported by further molecular phylogenetic research (Potter et al. 2007 and others). Ertter & Reveal (2014) preferred to retain *Duchesnea* as distinct because of its condensed shoot structure at stolon nodes, enlarged 3-lobed epicalyx bractlets, and accessory fruit structure, but others (e.g., Weakley 2015; Kartez 2018) have accepted its position within *Potentilla*.

Potentilla indica was reportedly introduced to the USA as a medical and ornamental plant (Ertter & Reveal 2014). The species is an herbaceous perennial that has spread over most of eastern continental USA to central Texas, eastern Oklahoma, Kansas, Nebraska, and Wisconsin. It is absent from the New England states except for Connecticut, and the western Great Plains and mountain states of the west, but it is recorded in California, Oregon, and Washington (Hitchcock et al. 1969; Ertter & Reveal 2014). The species has also become naturalized in Africa, Australia, Europe, and South America (Ertter & Reveal 2014). As a weed, *P. indica* does not appear to have noxious possibilities in terms of ecological stability in North American plant communities.

Based upon the following specimen, we report *Potentilla indica* as new to the naturalized flora of Utah.

Utah. Weber Co.: South Ogden, scattered in lawns and edges of shaded woodlands, 0.2 mi E of jct of Hwy 98 and E5425 S Street and in lawns and shaded woodland edges of cul-de-sac on E 5375 S Street, 26 Jul 2017, *J.R. Singhurst 21,184* with Liz, Ava, and Ruby Singhurst (BAYLU). Figures 1 and 2.

Multiple populations of *Potentilla indica* were growing in the South Ogden area in shaded lawns and shaded edges of mountain oak woodlands under an overstory of *Acer grandidentatum*,

Amelanchier alnifolia, *Berberis repens*, *Cercocarpus montanus*, *Prunus virginiana*, *Quercus gambelii, Rosa* sp., and *Symphoricarpos oreophilus*. Herbaceous flora associated in close proximity included *Cirsium arvense*, *Epilobium ciliatum*, *Glechoma hederacea*, *Poa annua*, *P. pratensis*, *Plantago lanceolatum*, *Taraxacum officinale*, and *Tragopogon dubius*. Although distinguishing individual plants was difficult (the plants spread vegetatively by stolons), the number of plants in flower and fruit at the voucher site was estimated as 35 to 50 (Figs. 1 and 2).

Discussion

Anthropogenic modifications of the Great Plains have promoted plant distributions expanding from the eastern USA (Mink et al. 2010). The fruit is not sweet, which may affect dispersal by mammals and birds. Box turtles (*Terrapene carolina*) are known consumers and dispersers of *Potentilla* fruit and seed in localized habitats (Braun & Brooks 1987). Native migratory passerines as vectors of distributional expansion has been described (Mink et al 2015).

A widely distributed passerine that migrates both latitudinally and altitudinally throughout the USA distribution of *Potentilla indica* (Alderfer et al. 2014) is the American Robin (*Turdus migratorius*). This species has significantly expanded its range in the last 50 years (Eiserer 1976; Ehrlich et al. 1988; Alderfer et al. 2014), especially in areas where trees are planted, structures erected, and water distributed, thus creating suitable habitats and nesting sites. The American Robin is one of the most abundant birds in the Utah, from the lowlands into mountains of the Uintah and Wasatch ranges and Uintah Basin (Behle 1981). Population increases in a post-DDT era also have led to its range expansion (Knupp et al.; Ehrlich et al. 1988). This North American passerine is a known frugivore which readily feeds from the ground (Paszkowski 1987; Wheelwright 1986) and prefers to forage in irrigated landscapes.

Figure 2. *Potentilla indica* in Weber Co., Utah, 26 July 2017. Photograph by J.R. Singhurst.

Figure 2. *Potentilla indica* in Weber Co., Utah, 26 July 2017. Photograph by J.R. Singhurst.

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TAXONOMY OF *PAPAVER* SECT. *MECONELLA* (PAPAVERACEAE) IN BRITISH COLUMBIA

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ABSTRACT

Native and exotic North American species of *Papaver* sect. *Meconella* (Papaveraceae) are discussed, with a geographical focus on British Columbia, Canada. *Papaver alboroseum, P. lapponicum, P. macounii, P. nudicaule,* and *P. radicatum* are found to be misapplied names in British Columbia, and of these, only *P. lapponicum* (subsp. *occidentale*) and *P. macounii* are found to occur North America. Species of *Papaver* sect. *Meconella* accepted for British Columbia are the exotic *P. croceum* and the native *P. hultenii, P. kluanense, P. pygmaeum*, and the novel species **P. columbianum** Fedde ex Björk**, sp. nov.**, **Papaver luculentum** Björk**, sp. nov.**, and **Papaver roseoalbum** Björk, **sp. nov.** One additional native, unnamed taxon is also discussed, referred to as *Papaver* "unknown 1." A key is presented to *Papaver* sect. *Meconella* of British Columbia. The neglected species *P. coloradoense* is also discussed.

The present paper is the first in a series of studies intended to clarify taxonomy of vascular plants in British Columbia (BC), Canada, toward a soon-to-be-published manual. This study focuses on Papaveraceae, especially the acaulescent arctic-alpine poppies, *Papaver* sect. *Meconella* Nutt. (Carolan et al. 2006). It accounts for all acaulescent arctic-alpine species of the genus and all of the species treated herein. Sect. *Meconella* poppies have been a long-standing challenge to taxonomists, due in part to the remote locations of most populations of the section. It is difficult and expensive to travel to the mostly tundra habitats in northern mountain ranges and in the arctic to study the plants in the field, and herbarium specimens are few and often of poor quality. Pressed specimens of sect. *Meconella* are not ideally revealing of phenotype, since leaf and petal colour do not preserve well and the petals usually fall quickly after collecting and are often absent. Confusion has also arisen from misinterpretations of type specimens or resulting from needs for lectotypification.

A taxonomic model can be greatly clarified by increasing the names available to apply to species in order to reduce the confusion that arises from misapplications using unsupportably broad species concepts. The present descriptions of new species and the resurrection of neglected names are intended in part to serve that purpose.

For the present study, all sect. *Meconella* specimens from the two main herbaria of British Columbia (UBC and V) were examined, as well as loan material of *Papaver alboroseum* from the herbarium ALA and high-resolution scans of types and other important early collections. Type specimen scans examined (ITHAKA 2016) are all shown with a ruler for scale and a colour swatch for hue calibration. All photographs shown are by the author. The species accepted for the British Columbia flora are listed first, in order of publication date. Species rejected from the British Columbia flora are presented in an annotated list, and notes on other related species of sect *Meconella* of western North America are provided.

Papaver sect. *Meconella* in British Columbia

1. PAPAVER CROCEUM Ledeb., Fl. Altaica 2: 271. 1830. **TYPE:** not seen. No specimens are cited in the protologue; lectotypified on an illustration in Dillenius (Hortus Elthamensis t. 224 f. 291), which in turn was based on a plant from the Altai Mountains.

This species is a core ancestor of cultivar lineages, giving us the so-called "Iceland poppy" sold in nurseries as a spring annual or short-lived perennial (Elven et al. 2018). Specimens and garden tags on these plants often bear the erroneous identification as *P. nudicaule* L., but *P. croceum* has been shown to be the correct name for the cultivated plants (Hanelt 1970). It occasionally escapes from cultivation or is deliberately seeded along roadsides or into meadows. It can be recognized by its lax growth form and large leaves and its large, bright yellow, orange or red petals.

2. PAPAVER PYGMAEUM Rydb., Bull. Torrey Bot. Club 29: 159. 1902. *Papaver radicatum* var. *pygmaeum* (Rydb.) S.L. Welsh, Great Basin Naturalist 46: 259. **LECTOTYPE** (designated here**): USA. Montana.** Mountain above Stanton Lake, 1 Aug 1894, *Williams 992* (NY 99719! [scan viewed online]). No holotype designated by Rydberg; Fedde used *Macoun 10269*, the second of three specimens cited by Rydberg, as the type of *P. nudicaule* subsp. *radicatum* var. *pseudocorydalifolium*, which is clearly a superfluous taxon.

Papaper nudicaule subsp. *radicatum* var. *pseudocorydalifolium* Fedde, Repert. Sp. Nov. Regni 7: 256. 1902. **TYPE: CANADA. Alberta.** Sheep Mountain, 1895, *Macoun 10269,* (US 99718! [scan viewed online]). No holotype designated by Fedde. Specimen cited by Rydberg in description of *P. pygmaeum*.

Plants scapose perennials from a tightly branched caudex, caespitose. **Leaves** dark green or somewhat glaucous, setose-hirsute or glabrate, blades ovate to ovate-deltate in outline, < or = petioles, most or all 2x pinnate, primary lobes in 2–3 pairs, obovate to oblanceolate, nearly or quite contiguous or even overlapping, apices mostly rounded to blunt, bristle-tipped or not. **Petiole bases** withering but persistent, dark brown or blackish. **Scapes** ascending to erect, 3–6(–12) cm, setose-hirsute, hairs mostly spreading, stramineous or light brown. **Sepals** caducous, densely setose-villous, hairs medium to dark brown. **Petals** caducous after anthesis, yellow, salmon or reddish orange, often bicoloured orange and (proximally) yellow, 6–10 mm, obovate-obdeltate to elliptic, ca. 1.5x ovary length. **Stamens** ca. 15–20, anthers yellow, aging to brown. **Stigmatic disc** conic, not umbonate, lobes 4–5, not winged. **Capsule** obovate to elliptic, 9–15 mm long, setose, hairs ascending-appressed, stramineous. **Seeds** not observed.

Papaver pygmaeum has unusual attributes among native North American members of sect. *Meconella*. Its combination of deep yellow, orange, or sometimes almost red flowers and its stramineous capsule hairs are unique among native British Columbia *Papaver*, and the comparatively dark green leaf colour and crowded, mostly obovate leaf lobes give an unusual appearance to the leaves of this species. It is very limited in distribution, being found in the Waterton/Glacier National Parks region in Alberta and Montana and rarely into British Columbia on the crest of the Rocky Mountains in the extreme southeast corner of the province. See also notes under *P. coloradense*, below.

Other specimens studied. **CANADA**. **Alberta**. Dorner Pass, 7500 ft, 16 Aug 1945, *Cowan s.n.* (UBC 47978!); Waterton Lakes Park, rock slide below Carthew Lake, 7500 ft, 8 Jul 1951, *Taylor 8677* (UBC 21855!). **British Columbia**. Akamina Ridge, 2440 m, 12 Aug 1976, *Pojar 760429* (V 94587!). **USA**. **Montana**. Open rocky slope, along the trail from Many Glacier Hotel to Piegan Pass, 1500-2600 m, 11 Aug 1919, *Standley 17496* (UBC 98245!, mounted photograph of specimen at DAO).

3. PAPAVER KLUANENSE D. Löve, Bot. Not. 109: 178. 1956. *Papaver radicatum* subsp. *kluanense* (D. Löve) D.F. Murray, Novon 5: 294. 1995 (as subsp. *kluanensis*). **TYPE: CANADA. Yukon Territory**. North of Quill Creek Camp, alt. ca. 5000 ft, 20 mi W of Burwash Landing, 15 Jun 1953, *Freedman s.n.* (S S08-261! [scan of fragments and a photograph of the type]). Orthographic correction to the originally published name *Papaver kluanensis*. No holotype designated by Löve.

Papaver freedmanianum D. Löve, Bot. Not. 109: 184. 1956. **TYPE: CANADA. Yukon**. North of Upper Quill Creek, 20 mi W of Burwash Landing, 6000 ft, 18 Jun 1953, *Freedman s.n.* (S S-G-4525! [scan of fragments and a photograph of the type]). No holotype designated by Löve.

Papaver nigroflavum D. Löve, Bot. Not. 109: 180. 1956 (as *P. nigro-flavum*). **TYPE: CANADA. Yukon Territory.** North of Tetamagouche Pass, 20 mi W of Burwash Landing, ca. 5000 ft, 5 Jul 1953, *Freedman s.n.* (S S-G-4533! [scan viewed online]). No holotype designated by Löve.

Plants scapose perennials from a tightly branched caudex, caespitose. **Leaves** greyish green, blades ovate to elliptic in outline, < or = petioles, most or all 1x pinnate, segments usually 5, elliptic-oblanceolate to narrowly elliptic, nearly or quite contiguous, apices mostly acute. **Petiole bases** marcescent, light to medium brown. **Scapes** ascending to erect, 6-15(-20) cm, hirsute to setose-hirsute, hairs mostly erect or ascending, medium to dark brown. **Sepals** caducous upon anthesis, densely setose-villous, hairs medium to dark brown. **Petals** caducous at anthesis or sometimes irregularly withering around the ovary, creamy yellow, 6-7 mm, broadly obovate-obdeltate, 1.5-2x ovary length. **Stamens** ca. 25-30. **Stigmatic** disc low-convex, not umbonate, lobes 5-6, not winged. **Capsule** broadly obovate-elliptic to broadly obovate, 10-13 mm long, setose, hairs ascending-appressed, dark brown. **Seeds** not observed.

Papaver kluanense has been treated in a broad sense by Kiger & Murray (1997) and others. Reports of the species from the U.S. Rocky Mountains are all or mostly *P. coloradoense* (see notes, below). Some plants from the Beartooth Plateau of Montana and Wyoming may be *P. kluanense*, but the specimens from there are too few to address this question. See for example: Wyoming, Park County, Shoshone National Forest, Beartooth Plateau area just south of Montana border and west of highway 212 on switchbacks ca. 0.75 miles ENE of Beartooth Pass, 11 Jul 1990, *Henderson 7808* (ID 118551! [scan viewed online]).

Papaver columbianum (as *P. nudicaule* var. *columbianum*) occurs entirely within the range of *P. kluanense* and has long been treated as a synonym, despite its distinctive characteristics. The name *P. kluanense* has also been applied variously to other dissimilar species in British Columbia. The name should apply only to short, caespitose plants having all mostly 1x pinnate leaves with strongly ascending, closely spaced, acute segments, uniformly coloured and caducous petals, and more or less obovate capsules.

Selected specimens studied. **CANADA**. **Alberta**. Mount Southesk, 4 Aug 1943, *Cowan s.n.* (V 163300!); Banff National Park, Merlin Ridge, 31 Jul 1962, *Shulman 3483* (V 73676!); on the Whistler, Jasper Park, 2 Aug 1964, *Munday s.n.* (UBC 108946!). **British Columbia**. 8 Mile Creek, Toad River Lodge, Liard River, Alaska Highway, mile 437, 15 Jul 1959, *Zielger s.n.* (V 33851!); western slope of Mount Edziza, 12 Aug 1971, *Brayshaw s.n.* (V 58567!); upper plateau, S side of Birch Mountain, Teresa Island, Atlin Lake, 1 Aug 1974, *Buttrick 5509* (UBC 159538!); Potentilla Ridge, between Danihue Pass and the headwaters of Cullivan Creek, 10 Jul 1975, *Pojar s.n.* (UBC 155548!); Solifluction Ridge, Gladys Lake area, 11 Aug 1975, *Pojar s.n.* (UBC 155545!); Relay Creek Cabin, 23 Jul 1977, *Selby 540* (UBC 166293!); Kusawak Range, 25 Jul 1979, *Douglas 11440* (V 96282a! and b!); near summit of Bull Moose Mountain, NW of town of Tumbler Ridge, 28 Jul 1991, *Straley 6877* (UBC 226719!); ridge SW of Squaw Creek, Haines Triangle, 28 Jul 1992, *Pojar JP920212* (V 175944!). **Yukon Territory**. Deazdeash Mountains, Mt. Decoeli, 4 Jul 1943, *Brink s.n.*

(UBC 120982!); Mount St. Elias Quad, Outpost Mountain at S end of Kluane Lake, 18 Jul 1971, *Murray 3009* (V 136112!); Marble Creek (N of), ca. 26 mi SSW of Haines Junction, 27 Jul 1973, *Douglas 6494* (V 87571a! and b!).

4. PAPAVER HULTENII Knaben, Opera Bot. Čech. 3: 49. 1959. **TYPE: USA. Alaska.** Northern Coastal Plain, Meade River Village, 5-8 Aug 1960, *Stone s.n.* (DAO 336965! [scan viewed online]).

Plants scapose perennials from a simple root crown or somewhat branched caudex, tufted. **Leaves** greyish green, blades < or = petioles, 1x pinnate, or a few segments shallowly notched, segments 5-7, narrowly oblanceolate, narrowly lanceolate or almost linear, widely spaced, apices mostly acuminate. **Petiole bases** marcescent, medium brown. **Scapes** ascending to erect, (10-)20-40 cm, setose-hirsute to strigose, hairs mostly ascending to appressed, mostly dark brown. **Sepals** caducous, densely setose-villous, hairs dark brown. **Petals** caducous or withering irregularly around the capsule, apparently yellow, often bruising blue-black, 15-25 mm long, obovate-obdeltate, 2-2.5x long as ovary. **Stamens** ca. 30-40. **Stigmatic disc** conic, not distinctly umbonate, lobes 5-6, not winged. **Capsule** oblong-oblanceolate, 15-19 mm long, setose, hairs ascending-appressed, dark brown. **Seeds** not observed.

This tall species can be recognized by its usually long, lax petioles, narrow, widely spaced and usually simple leaf lobes, its oblong-oblanceolate capsules, and its mostly appressed, dark brown hairs on the scapes. Like *Papaver alaskanum, P. denalii, P. luculentum,* and *P. mcconnellii* (see below), it has marcescent petioles that cloak the caudex branches. But unlike those species, *P. hultenii* has a more lax, tufted growth unlike the densely caespitose growth form of the above species. It is also similar to *P. kluanense,* especially in the shape of the leaf lobes, but those lobes are more widely spaced, and the plants are taller and have a more laxly branched caudex. Perhaps most similar to *P. hultenii* is the Seward Peninsula form of *P. denalii*; they may be conspecific.

An arctic-alpine species, *Papaver hultenii* is apparently the only *Papaver* that occurs both in British Columbia and the Arctic. All British Columbia specimens known so far are from Pink Mountain, an alpine ridge in the eastern Rocky Mountain Front Ranges in the boreal northeast of the province.

Selected specimens examined. **CANADA**. **British Columbia.** Pink Mountain, Upper Halfway River, Jul 1957, *McLaughlin s.n.* (V 33163!); Summit of Pink Mountain, Alaska Highway, 28 Jul 1990, *Straley 6204* (UBC 202401!); Pink Mountain, Peace River District, 16 Sep 1980, *Rose AAR80436* (UBC 170125!); Pink Mountain lookout road near summit of Pink Mountain, 10 Aug 1993, *Lomer s.n.* (UBC 43835!); Pink Mountain, Peace River, 13 Jul 2009, *Roemer HR09010* (V 206445!). **Yukon Territory.** Ogilvie Mountains, mountain E of mile 50-54, 27 Jun 1966, *Porsild 19* (UBC 119334!); about 100 mi up Dempster Highway from Whitehorse to Dawson City Highway, 10 Jul 1976, *McComb s.n.* (UBC 160869!); British Mountains, tributary of Firth River, 7 Jul 1980, *Cody 27143* (UBC 213053!); Km 142, Dempster Highway, 17 Jul 1980, *Cody 27986* (UBC 213051!); Dawson Quad, Ogilvie Mountains, North Fork Pass and vicinity, Dempster Highway, 8 Jul 1984, *Parker 1190* (ALA 81044! scan). **USA. Alaska.** Harrison Bay Quad, National Petroleum Reserve, vicinity of Fish Creek test well 1, 27 Jul 1977, *Murray 6631* (ALA 78755! scan); near mile post 111-3 on Prudhoe Bay Road, 7 Aug 1980, *Ostler 2162* (V 137326!); Philip Smith Mountains Quad, Dalton Highway, mile 276, 30 Jul 1982, *Murray 8561* (ALA 76966!); Noatak Quad, Cape Krusenstern (Sealing Pt.), vic. 2-8 km N of VABM Krusenstern, 11 Jul 2002, *Parker 12040* (ALA 139600 scan); Eagle C6 Quad, middle fork of the Charley River, peak on ridge dividing east and middle forks, 16 Jul 2002, *Roland 5646* (ALA 149428 scan); White Mountains of interior Alaska, 12-Mile Summit, between Circle and Fairbanks, 23 Jun 2010, *Fulkerson 75* (SRP 47635! scan).

5. PAPAVER COLUMBIANUM Fedde ex Björk, **sp. nov. TYPE: CANADA. British Columbia.** Mountains at Kicking [Horse], [possibly Yoho National Park], 8000 ft, 14 Aug 1890, *Macoun s.n.* (holotype: US 99717! [scan viewed online]). Figures 1–2.

The name *Papaver columbianum* was first published illegitimately by Fedde as a nomenclatural synonym in his protologue of *P. nudicaule* var. *columbianum* Fedde, Pflanzenr. (Engler) 40: 378. 1909.

Species habitu et folia *Papaver kluanense* similis sed petala ad maturitatem fructus persistens et petalorum basis nigrescentibus differt.

Plants scapose perennials from a tightly branched caudex, caespitose. **Leaves** greyish green, blades < or = petioles, most or all 1x pinnate, segments usually 5, oblanceolate to elliptic-lanceolate, nearly or quite contiguous, apices mostly acute, petiole bases marcescent, medium brown. **Petiole bases** withering, not conspicuous. **Scapes** ascending to erect, to 3-10 cm, setose-hirsute, hairs mostly spreading, light (proximal) to dark (distal) brown. **Sepals** sometimes persistent, densely setose-villous, hairs medium to dark brown. **Petals** persistent past anthesis, apparently opening yellow, aging to bicolored black and whitish, 6-7 mm, obovate-obdeltate, < to = ovary. **Stamens** ca. 20. **Stigmatic disc** convex, not umbonate, lobes 4-5(-6?), not winged. **Capsule** broadly obovate, 8-10 mm long, setose, hairs ascending-appressed, dark brown. **Seeds** medium red-brown, ca. 0.7 mm, reticulate-ridged, ridges sinuous, demarcating irregularly polygonal pits.

Among western North American *Papaver*, this species is unusual in having petals that are persistent without withering and that are shorter than to equal to the ovary, and the sepals sometimes also persist into anthesis. All other native *Papaver* in the region have quickly caducous sepals (dropping by the onset of anthesis) and petals (dropping at the end of anthesis or sometimes irregularly withering around the ovary). It is also unusual among regional *Papaver* in that the petals (at least with age) become bicolored: black proximally and whitish distally. It may be most closely related to *P. kluanense,* sharing leaf characteristics and having similar geographical distribution and habitat.

Figure 1. Flowers of *Papaver columbianum.* Left, UBC 242379. Right UBC 222563). Scale bars = 3 mm.

Figure 2. *Papaver columbianum* (UBC 242379).

Papaver columbianum may be rare; only three specimens are known besides the type. However, the widely separated localities and the remote, difficultly accessed intervening mountain ranges suggest that more populations may be expected. It is probably strictly alpine in its ecology. Associated species reported to occur with the Alberta population are *Antennaria monocephala, Askellia pygmaea* (Ledeb.) Sennikov, *Cerastium beeringianum*, *Claytonia megarhiza*, *Draba spp., Erigeron lanatus*, *Erysimum pallasii*, *Phacelia sericea*, and *Saxifraga adscendens*.

Other specimens examined. **CANADA**. **Alberta**. Banff National Park, Lipalian Mountain, Purple Mound, wind-swept alpine slopes, 2460 m, 13 Jul 2013, *Scotter BNP 001* (UBC 242379!). **British Columbia**. Redfern-Keily Provincial Park, Rocky Mountains, Muskwa Ranges, Redfern Mountain, 25 Jul 2014, *Marr 14-0083* (V 215119!). **Yukon Territory**. Sheep Mountain, near Kluane Lake, SW plateau, 6000-6327 feet, 18 Jul 1970, *Krajina s.n.* (UBC 222563!).

6. PAPAVER LUCULENTUM Björk, **sp. nov. TYPE: CANADA. British Columbia.** Boundary Ranges, ridge N of North Treaty Creek, near Bowser Lake, W of Bell Irving River, 56° 38'6.88"N 129° 52'13.18"W, on fine argillite gravel scree, windblown alpine ridge, 4 Jul 2013, *Björk 32373* (holotype: UBC!). Figures 3-4.

Species habitu cum *Papaver mcconnellii* sed differt fructuum subsphericis et umbo stigmatosum deficiens; differt a *Papaver denalii* foliis vere bipinnatis et petala minoribus.

Plants perennial, caespitose, slightly glaucous, hirsute and strigose, hairs white to brown, scapose, (10-)15-25(-30) cm. **Leaf blades** ovate in outline, 2(-3)x pinnately lobed, segments ovate to oblong-elliptic, primary lateral segments 1(-2) pairs, apices mostly blunt, bristle-tipped. **Petiole bases** withering, not conspicuous. **Scapes** nodding in bud, decumbent or sinuous, apex abruptly widened, strigose with appressed, crisped ivory (mostly proximally) and dark brown more setose (mostly distally) hairs. **Sepals** caducous, hairy like the scapes. **Petals** pale yellow, sometimes with a pink blush (drying deeper yellow), 19-22 mm (longer when fresh), not bruising blue-black after handling and pressing. **Stamens** 30-42, filaments creamy yellow, anthers creamy yellow, aging to brown. **Stigmatic disc** convex, stigma lobes 6-8. **Capsules** broadly obovate to subspheric, 9-12 mm long (larger when fresh), previous years' capsules narrower, ascending to erect, obscurely ribbed, ribs becoming more distinct with fruit maturation, setose with ascending, brown hairs, hairs broadened proximally, but not pustular-based. **Seeds** medium reddish brown, ca. 1 x 0.6 mm, finely ridged longitudinally, not appendaged or winged.

Paratypes. **CANADA. British Columbia.** North Kitseguela Creek, Hazelton District, Jul-Aug 1952, *Harrison s.n.* (UBC 64942!); Spectrum Mountains, Cassiar, Jul 1957, *Harrison s.n.* (UBC 64928!); Focus Mountain, Taku River area, 12 Jul 1982, *Češka 12483* (V 167691!); Nimbus Mountain, Nakina Lake, N of summit, mountain W of lake, 6 Aug 2008, *Marr 08-1204* (V 203821!); Boundary Ranges, ridge N of North Treaty Creek, near Bowser Lake, W of Bell Irving River, 56° 39'9.4"N 129° 55'1.15"W, 7 Jul 2013, *Björk 32462, 32464, 32465* (UBC!).

Papaver luculentum is similar to the Alaskan species *P. alaskanum* and *P. denalii* Gjærevoll and the northern Yukon/Northwest Territories species *P. mcconnellii* Hultén. Like *P. luculentum,* all three are caespitose with a tightly branched caudex and with long-lasting marcescent petioles. *Papaver alaskanum*, known only from the Aleutian Islands, has darker green leaves with shorter hairs, and only dark brown hairs on the scapes. The type of *P. denalii* is representative of the numerous specimens at ALA (reviewed as scans) identified as that species and specimens collected from Denali National Park or elsewhere in the Alaska Range that are mididentified as *P. mcconnellii*. These differ from *P. luculentum* in having larger petals, mostly 1x lobed leaves, and sparser, more spreading hairs on the scapes. Plants identified as *P. denalii* or *P. mcconnellii* from the Seward Peninsula (west-central Alaska) further differ in having longer, almost linear leaf lobes. *Papaver*

mcconnellii, as applied only to plants from near the type locality on the Yukon/Northwest Territories border, differs from *P. luculentum* in having a sharp central umbo on the stigmatic disc, larger petals, more numerous stamens (ca. 50-60), and a narrower fruit shape (obovate). At least some specimens of *P. denalii* and *P. mccconnellii* also differ in having petals that bruise blue-black with handling.

Figure 3. Habit photo of *Papaver luculentum* at holotype location.

Some specimens of *Papaver luculentum* may resemble *P. roseoalbum* (see below), especially as the petals are similarly pale and sometimes pinkish. However, the bristles on the capsules of *P. luculentum* are medium to dark brown, not ivory, the hairs on the scapes lack the characteristic purplish and white coloration, and *P. roseoalbum* does not have long-lasting marcescent petioles or such a widely branched caudex as *P. luculentum*.

Figure 4. Upper: flowers and fruit of *Papaver luculentum*. Lower: detail of leaves, all from the type locality.

I know of *Papaver luculentum* only from the Cassiar and Boundary Ranges in the southern portions of northwest British Columbia, close to the border with Alaska, where it should be sought. I have not found this species during extensive alpine exploration in the Skeena Mountains, the range immediately east of the Cassiar/Boundary Ranges, nor in the Coast Ranges to the south. Other collectors' specimens are not numerous, and all are from the same region of northwest British Columbia. Hence, the species may be rare.

At the type locality, *Papaver luculentum* occurs on sparsely vegetated scree on windward (west to south) slopes of alpine ridges. Parent rock material is black argillite, which is almost ubiquitous at all elevations of that portion of the Boundary Ranges. The presence in the local flora of numerous calciphilic species and the high pH of nearby wetlands suggest the argillite is moderately calcareous. Winter snow accumulations are very high in the Boundary Ranges, but most likely the sites occupied by *P. luculentum* are less snow-covered than surrounding subalpine areas due to exposure to wind. Associated species are of the genera *Aconitum, Agoseris, Epilobium, Myosotis*, *Oxyria*, *Poa, Polemonium*, *Potentilla*, and *Saxifraga.*

Selected specimens of *P. denalii* s. str. studied, Alaska Range form. **TYPE: USA. Alaska.** Alaska Range, McKinley Park, Cathedral Mountain, in scree slopes, abundant, 20 Jul 1959, *Gjærevoll 2412* (TRH! photographs). **Others**: Norton Bay Quad, Nulato Hills, upper Unalakleet River valley, 3 Jul 1998, *Parker 8087* (ALA 125108! scan); Lime Hills Quad, Nushagak-Big River Hills, Lyman Hills, 7 km NW of VABM Utica, 1 Jul 1999, *Parker 8961* (ALA 128252! scan); Mount McKinley Quad, Alaska Range, ridge N of the W fork of the Herron Glacier, 9 Jul 1999, *Duffy MD99-46* (ALA 148286! scan); Mount Healy Quad, Alaska Range, Easy Pass on upper Bull River, 24 Jun 2000, *Duffy MD00-30* (ALA 147668 scan); Healy Quad, Alaska Range, W side of Easy Pass, 12 Jul 2000, *Duffy MD00-95* (ALA 147733 scan); Talkeetna Quad, Alaska Range, Shellabarger Pass, 2.2 km NE of ponds in pass, 1 Aug 2001, *Duffy MD01-126a* (ALA 148087! scan); Eagle D-4 Quad, Yukon-Charley Rivers National Preserve, ridge 2.4 km E of Mt. Sorenson, Yukon-Tanana Uplands, 30 Jun 2002, *Larson 02-1648* (ALA 83597! scan); Talkeetna Quad, Alaska Range, upper Tatina River Valley, 9 Jul 2002, *Duffy MD02-38* (ALA 148786! scan).

Selected specimens of *P. denalii* s. lat. examined, Seward Peninsula form. **USA**. **Alaska**. Hooper Bay Quad, Clarence Rhode NWR, 23 Jul 1975, *Boise 023* (ALA 66840! scan); Bering Strait District, hills adjacent to the Kukpuk River, Flint Mountain and surrounding hills, 15-16 Aug 1959, *Johnson 699* (ALA 9290! scan); Teller Quad, Seward Peninsula, N fork Grand Central Creek, 6 Jul 1996, *Murray 12192* (ALA 129001! scan); Solomon Quad, Seward Peninsula, Big Creek Valley, 23 Jul 1993, *Murray 11762* (ALA 158196! scan).

Selected specimens of *P. mcconnellii* s. str. examined. **CANADA**. **Yukon Territory.** Richardson Mountains, 6 Jul 1982, *Cody 30418* (ALA 103936! scan); Richardson Mountains, on N side of Dempster Highway, K465 (campground), 4 Jul 1982, *Cody 30152* (ALA 103941 scan!); Ogilvie and Wernecke Mountains, 12 mi NNE of Chapman Lake, W of Blackstone River, 8 Jul 1984, *Cody 33873* (ALA 102507! scan); Mackenzie Mountains, mountain E of Dempster Highway 414 km, 20 Aug 2003, *Solstad 03/0622* (ALA 154052! scan); Knorr Range, lakes at headwaters of Noisy Creek, 10 Jul 2005, *Bennett 05-0376* (ALA 157401! scan).

7. PAPAVER ROSEOALBUM Björk, **sp. nov. TYPE: USA. Alaska.** *Populus-Alnus* thicket, at mouth of small canyon, W of Portage Glacier, 12 Jul 1968, *Welsh 8146* (ALA 274045!). Figures 5-7.

Species americanas boreali quam *Papaver alboroseum* camtchatcensis affinibus sed petala grandibus, pilorum longioris et albo-purpureis bicoloratis, foliis bipinnatifidis, et folia lobis pro parte maxime ellipticis vel oblanceolatis differt.

Plants perennial, apparently short-lived, caespitose, scapose, 8-25 cm, greyish green, strigose, setose and villous, hairs at apex of scape brown and spreading, those elsewhere on the scape and on the leaves bicolored white and brownish purple, 1-3 mm, those of the leaves mostly bicolored white and purple-brown, 0.5-1.5 mm. **Leaf blades** ovate in outline, at least some 2x bipinnatifid to bipinnate, segments mostly elliptic to oblanceolate, primary lateral segments mostly 2 pairs, apices mostly blunt, bristle-tipped. **Petiole bases** withering, not conspicuous. **Scapes** nodding in bud, decumbent or sinuous. **Petals** whitish pink to pink or apricot, drying yellowish, 11-20 mm, not or only obscurely bruising blue-black after handling and pressing. **Stamens** ca. 15-25, filaments creamy

yellow, drying sordid green, anthers creamy yellow, aging to brown. **Stigmatic disc** convex, umbo lacking, lobes 6-8. **Capsules** obovate to elliptic, (5-)8-11(-13) mm long, ascending to erect, obscurely ribbed, ribs becoming more distinct with fruit maturation, hairs firm, bristle-like, ivory to pale brown. **Seeds** medium reddish brown, reniform, ca. 0.8 mm, surface reticulate-pitted, demarcating longitudinally rectangular pits.

Etymology: Latin *roseo-* (pink) and *-album* (white), an anagram of the similar and probably related Russian species *Papaver alboroseum*. For a mnemonic, the species arrayed geographically with north at the top of the map, *P. alboroseum* on the left and *P. roseoalbum* on the right are also arrayed alphabetically.

Paratypes. **CANADA**. **British Columbia.** Crest of ridge at limit of vegetation, Spectrum Mts., Cassiar, 6000 ft, Jul 1957, *Harrison s.n.* (UBC 64929!); Exposed, S-facing, very fine scree slope, with no other vegetation, sub-alpine to high alpine, on mountain behind Kitchener Camp, ca. 6,500 ft, summer 1980, *Pojar s.n.* (UBC 193093!); Skeena Mountains, Spatsizi Plateau, Brothers Lake, NW of lake, 26 Jul 2009, *Marr 09-0770* (V 205481!); Nass River, Mount Beirnes, along SW ridge 1 km S of peak, 1977 m, 29 Jul 2005, *Marr 05-0360* (V 194657!). **USA**. **Alaska.** Ft. Richardson, 15 Jun 1948, *Spetzman s.n.* (ALA 201944!); between Rocky and Victor Creeks, Kenai Lake, Kenai Peninsula, 60° 21'N 149° 21'W, common in open gravel-shale areas by lake, flowers rose-white, 2 Jul 1951, *Calder 5575* (V 136128!); Portage Glacier, 15 Jun 1959, *Gjærevoll s.n.* (ALA 24989!); Portage Glacier flats, 9 Jul 1964, *Williams 749* (ALA 201945!); Portage, 7 Jul 1965, Welsh 4560 (ALA 247976!); foot of Eklutna Glacier, 12 Jul 1965, *Welsh 4644* (ALA 201946!); W of Portage Glacier, 12 Jul 1968, *Welsh 8146* (ALA 274045!); Stikine Mountain Flora, immediately W of Kitchener Crag, SW of Kitchener Lake, Toodoggone River Quadrangle, 27 Jun 1969, *Rigby 98* (ALA 62009!); Bonanza Ridge, Wrangell Mountains, 5 Jul 1976, *Schmitt 160* (ALA 77486!); Bonanza Ridge, Wrangell Mountains, 6 Jul 1976, *Schmitt 166* (ALA 77485!); Mt. McKinley Quad, W fork of Big Stoney Creek, 25 Jun 1977, *Hutson s.n.* (ALA 98639!); Lower Llewllyn Glacier, Camp 26 and Marble Mountain Nunataks, 13 Aug 1977, *Anderson 3123* (ALA 90117!); Mount McKinley Quad, W fork of Upper Big Stony Creek, Mount McKinley, 28 Jun 1979, *Carwile 79-143* (ALA 87886!); Chugach National Forest, 3/4 mi down road from Portage Visitor Center, 30 Jul 1980, *Helmstetter 80-328* (ALA 72337!); municipality of Anchorage, Chugach State Park, Eklutna Valley, 1/4 mi N of Eklutna Glacier, 18 Jul 1984, *Marvin 1699* (ALA 84409!); Mount Hayes Quad, Rainbow Ridge vicinity, 2 Aug 1985, *Parker 1710* (ALA 82188!); Anchorage Quad, Chugach Mountains, North Campbell Creek Canyon, SE of Campbell Lake, 19 Jul 1994, *Lichvar 8093* (ALA 119363!); Healy Quad, Alaska Range, Dunkle Mine area, 13 Jul 2000, *Duffy MD00-105* (ALA 147743!); Anchorage Quad, Chugach Mountains, Knik River drainage, upper Hunter Creek, 19 Jul 2002, *Barker 02-696* (ALA 142313!); Seldovia Quad, Kenai Peninsula, Upper Nuka River, valley, E side of river, across from Nuka Glacier, approx. 10 km SE of Bradley Lake, 30 Jul 2003, *Lipkin 03-304* (ALA 152760!); Seward Quad, Kenai Peninsula, Exit Glacier, Harding Icefield Trail, 31 Jul 2003, *Sturdy 03-1309* (ALA 150819!); McCarthy Quad, Wrangell-St. Elias National Park and Preserve, above Kennecott Mine on trail to Bonanza Ridge and Jumbo Mine, 30 Jun 2005, *Dillman 2005-183* (ALA 246067!); Bering Glacier Quad, Chugach Mountains, E slope of Carbon Mountain, 9 Aug 2005, *Barker BG05-153* (ALA 156855!); Kenai Quad, Cook Inlet, W side, Saddle Mountain, North Lenore Hill, 29 Jul 2005, *Carlson 2005-54* (ALA 156321!); Portage Valley Site A, along the road leading W from the visitor center and to the sewage lagoon (beyond the bunkhouse), 24 Aug 2010, *Stephens AS-1* (ALA 171202!); Portage Valley Site B, around a fenced enclosure along the road leading W from the visitor center (before reaching the bunkhouse), 24 Aug 2010 *Stephens AS-2* (ALA 171203!); Milk Glacier, Chugach Mountains, 1 Aug 2012, *Nawrocki 12-003* (ALA 248725!); base of the N face of Mount Ascension, 15 Aug 2012, *Nawrocki 12-010* (ALA 248726!).

Figure 5. Holotype of *Papaver roseoalbum* (ALA 274045).

Figure 6. *Papaver alboroseum* (left, ALA 110037), and *P. roseoalbum* (right, ALA 77486), comparing the hairs of the scape. Scale bars = 2 mm.

Figure 7. *Papaver roseoalbum*. Upper, immature capsules (ALA 82188), scale bar = 2 mm.

At first appearance, *Papaver alboroseum* and *P. roseoalbum* are similar, but they can be distinguished easily by two consistent characteristics that correlate to the Asian and North American geographical ranges. While *P. alboroseum* has short, monochrome brown hairs on the scapes and only once pinnate leaves, *P. roseoalbum* has longer, white and purple-brown hairs on the scapes and at least some bipinnatifid leaves. Generally, the petals of *P. roseoalbum* average longer, and the capsules may on average have a broader shape, but there is much variation in these characters.

Ecology and geographical range. *Papaver roseoalbum* grows at low to high elevations. Reported habitats include sandy, gravelly soil, scree, and glacier forelands, often on volcanic substrates. I have not seen the species in the field myself. The holotype and each of the paratypes were originally identified as *P. alboroseum*. These specimens were all identified consistently, and because the petal colour of *P. roseoalbum* and pale fruit bristles are unusual among North American *Papaver*. It is likely that specimens I have not seen originally identified as *P. alboroseum* are probably not confused with species other than *P. roseoalbum*, hence, its range can be outlined as that of the misreports of *P. alboroseum*: south-central Alaska, far southwest Yukon, and far northwestern British Columbia. It is considered (under the name *P. alboroseum*) a conservation-priority species in British Columbia (BC Conservation Data Centre 2016). Plants under the name *Papaver alboroseum* in the rock garden nursery trade may sometimes be that species, but at least some plants in the trade identify as *P. roseoalbum*.

PAPAVER UNKNOWN 1

Plants perennial, long-lived, more or less caespitose, with numerous, moderately long caudex branches, cloaked in marcescent petiole bases, scapose, 10-25 cm, medium (greyish?) green, strigose, setose and villous, hairs of the scape medium to dark brown and mostly spreading, 1.5-3 mm, those of the leaves shorter and paler, 0.5-2 mm. **Leaf blades** ovate to elliptic in outline, 1x pinnate or with one or both of the lowest segments lobed, segments mostly narrowly elliptic to oblanceolate, sinuses moderately wide, primary lateral segments in 2-4 pairs, apices mostly acute, bristle-tipped. **Petiole bases** withering, not conspicuous. **Scapes** apparently erect in bud, erect in flower and fruit, usually 3-4x long as the leaves. **Petals** apparently yellow, 15-23 mm, bruising blue-black after handling. **Stamens** ca. 25-30, filaments creamy yellow, drying sordid green, anthers creamy yellow, aging to brown. **Stigmatic disc** low-convex, umbo lacking, lobes 6-8. **Capsules** oblong-oblanceolate, ca. 18-20 mm long, erect, conspicuously ribbed, hairs firm, bristle-like, ivory to pale brown. **Seeds** not observed.

Papaver unknown 1 occurs in alpine sites in far northern British Columbia. It appears similar to the illustration of *Papaver lapponicum* subsp. *porsildii* Knaben in the Flora of Alaska (Hultén 1968), except that the leaves usually have more lobes. I have not seen the type of that taxon. Elven et al. 2018 tentatively placed it in synonymy under *P. lapponicum* subsp. *occidentale* (C.E. Lundstr.) Knaben. Hultén usually had type specimens used as the models for the Papaver illustrations in the Flora of Alaska. If that is the case for *P. lapponicum* subsp. *porsildii*, then placement by Elven et al. (2018) is probably incorrect, as the illustration shows a morphology that suggests other relationships.

Papaver unknown 1 is similar to *P. hultenii* but has shorter scapes with widely spreading hairs and shorter and closer leaf lobes that are more abruptly contracted at the apex. From *P. kluanense* it differs in having narrower fruits, taller scapes, more distant leaf lobes and usually a less tightly branched caudex. I refrain from naming it as a new species pending further study.

Specimens studied. **CANADA**. **British Columbia.** Toad River, Toad River Lodge area microwave tower, mile 428 SW part of second and third hill, 22 Jul 1982, *Češka 13107* (V 167688!); Skeena Mountains, Klappan Mountain, along ridge 2 km W of Klappan Mountain summit, 4 Aug 2005, *Marr 05-0772* (V 195126!); Rocky Mountains, Muskwa Ranges, Terminal Range, mountain 7

km W of Muncho Lake, 2 Aug 2007, *Marr 07-0469* (V 200362!); Stikine Ranges, Blue Sheep Lake, summit E of "Little Blue Sheep" Lake, 12 Aug 2007, *Marr 07-1680* (V 202013!).

Names misapplied in British Columbia

PAPAVER ALASKANUM Hultén, Fl. Aleutian Islands, 190. 1937. **TYPE: USA. Alaska.** Aleutian Islands, Unalaska, 2 Aug 1932, *Hultén 7197* (S S-G-4519! [scan viewed online]). No holotype designated by Hultén.

This name has been misapplied to specimens of various species in British Columbia, among which *Papaver luculentum* (see below) is the most similar, sharing with *P. alaskanum* the marcescent petioles and 2x pinnately lobed leaves. *Papaver alaskanum* differs in having deeper yellow petals, darker green leaves, and dark brown hairs on the scapes.

PAPAVER ALBOROSEUM Hultén, Kungl. Svensk. Vet. Acad. Handl. 5: 141. 1928. **TYPE: RUSSIAN FEDERATION. Kamtchatka Australis.** Avatcha Volcano, 675 m, 30 Jul 1920, *Hultén 508b* (GB 0048356! [scan viewed online]; S S-G-4522! [scan viewed online]). No holotype designated by Hultén.

Papaver alboroseum var. *elongatum* Hultén, Fl. Kamtch. 2:141. 1928. **SYNTYPES**: **RUSSIAN FEDERATION. Kamtchatka Australis.** Toporkof Island, Sarannaja Bay, 8 Aug 1920, *Hultén 789* (GB 48357! scan). **Kamtchatka Orientalis**. Lake Assabatch [?], 1-15 Aug 1920-1922, *Malaise s.n.* (S S-G-4523! scan).

This species name has long been misapplied in North America. The Russian and North American specimens all differ consistently in pubescence and leaf lobation, and the populations of the two forms are widely separated geographically. See further notes under *P. roseoalbum*, above.

Other specimens studied. **RUSSIAN FEDERATION**. Kuril Islands, Sakhalin Oblast, Paramushir Island, mouth of Shimoiur River, 21 Jul 1979, *Barkalov s.n.* [or *3030*?] (ALA 110037!); Kuril Islands, Paramushir Island, mouth of Shimouir River, 21 Jul 1979, *Barkalov s.n.* [or *1676*?] (ALA 80350!); Kamtchatskiy region, Karaginskiy District, vicinity of village Ossora, 14 Aug 1976, *Kharkevich s.n.*, Plantae Vasculares Orientis Extremi Rossica Flora Exsiccata 144 (ALA 129009!).

PAPAVER KEELEI A.E. Porsild, Bull. Natl. Mus. Canada 101: 20. 1945. **TYPE: CANADA. Northwest Territories.** Canol Road, Mackenzie Range, small tributary to Little Keele River, mile 51, 8 Sep 1944, *Porsild 11782* (S S-G-4528! scan). No holotype designated by Porsild.

Other specimens studied. **CANADA**. **Yukon Territory**. Ogilvie Mountains, W of and in view of Dempster Highway, two drainages S of Distincta Peak, 15 Aug 2016, *Björk 41466* (Hb. Björk).

This distinctive arctic and northern boreal species is easily identified by its almost linear ovary. Even at maturity, the capsule is markedly narrow. It also has a distinctly dark color on dried herbarium specimens. It is also unusual in its preference for wet, mossy ground. Though habitat information is lacking on the label of the type specimen, the moist, mossy habitat can be deduced by the presence about the bases of the plants on the type sheet of moist-habitat mosses such as *Tomentypnum nitens* (Hedw.) Loeske. The occurrence of *P. keelei* in the southern portions of the Yukon suggests that it should be sought in northern British Columbia. See also notes under *P. macounii*, below.

PAPAVER LAPPONICUM (Tolm.) Nordh., Berg. Mus. Årbok 2: 45. 1931. *Papaver radicatum* subsp. *lapponicum* Tolm. **LECTOTYPE: RUSSIAN FEDERATION.** Murman area, Oz. Imandra, 1 Aug 1911, *Pohle s.n.* (LE, not seen).

Similarly to *Papaver radicatum,* this species name was misapplied in northwestern North America (Solstad 2009; Elven et al. 2018). In the region, the name *P. lapponicum* has been applied to specimens of a variety of dissimilar species. In British Columbia, the name was generally applied to species that average taller in stature than those that were identified as *P. radicatum*.

PAPAVER MACOUNII Greene, Pittonia 3: 247. 1897. **TYPE: USA**. **Alaska**. St. Paul Island, 23 Jul 1897, *Macoun s.n.* (C 10016380! scan, K 000653200! scan). No holotype designated by Greene.

Similar to *Papaver keelei, P. macounii* has a very narrow capsule, but it differs in its patent scape hairs and larger petals. Also, in comparison with *P. keelei* and with specimens of other North American *Papaver*, the leaves of *P. macounii* have a distinctly dark colour on herbarium specimens. This species has been applied to specimens of *P. hultenii* in British Columbia, which are similar to *P. macounii* in stature but with paler leaves and broader ovaries and capsules.

PAPAVER RADICATUM Rottb., Skr. Kiøbenhavnske Selsk. Laerd. Elsk. 10: 455. 1770. **EPITYPE** (designated by Nilsson & Elven in 2001) **ICELAND**. Bardastrandarsýsla, Brjánslæskur, 23 Jul 1962, *J.A. Nannfeldt 17564* (UPS 207575, not seen).

The typification of *Papaver radicatum* (discussed in Elven et al. 2018) clarified the species as one having a North Atlantic distribution. Even so, no taxonomic question in British Columbia was fully resolved by the typification, as the name *P. radicatum* was applied only as a catch-all for any of the shorter-stature native *Papaver* except the morphologically highly dissimilar *P. pygmaeum* and *P. roseoalbum*.

Key to *Papaver* sect. *Meconella* of British Columbia

1. Petals 50–90 mm long; stigmatic disc with 9–19 lobes; short-lived plants of disturbed sites, garden escape ..... **Papaver croceum**
1. Petals <50 mm long; stigmatic disc with 5–8 lobes; usually long-lived plants, always in wild sites, native.

2. Capsule hairs ivory white throughout; leaf lobes mostly obovate.

3. Petals mostly orange or red; far southeast ..... **Papaver pygmaeum**
3. Petals mostly white or pink; far northwest ..... **Papaver roseoalbum**

2. Capsule hairs medium to dark brown, at least in part; leaf lobes mostly elliptic, oblong, or (ob)lanceolate.

4. Young capsules several times longer than wide, with a sharp, pronounced umbo; plants often or always on wet ground; to be sought in British Columbia .....[*Papaver keelei*]
4. Young and mature capsules broader in shape.

5. Leaves all or nearly all 2x pinnately lobed; lobe apices rounded to blunt **Papaver luculentum**
5. Leaves all or nearly all 1x pinnate; lobe apices acute to acuminate.

6. Petals black proximally with age, white or whitish distally, persistent after flowering, < to = ovary ..... **Papaver columbianum**
6. Petals lacking proximal black blotches or irregularly bruising blue-black, otherwise yellow to salmon, falling or irregularly withering around the ovary after anthesis, > ovary.

7. Leaf lobes mostly contiguous; plants densely tufted; capsules 1–1.5x long as wide ..... **Papaver kluanense**
7. Leaf lobes mostly separated by wide sinuses; plants loosely tufted; capsules 1.5–2x long as wide.

8. Scapes mostly 20–40 cm, hairs mostly ascending to appressed; leaf lobes mostly acuminate ..... **Papaver hultenii**
8. Scapes 10–25 cm, hairs widely spreading; leaf lobes mostly acute... **Papaver unknown 1**

Notes on other *Papaver* sect. *Meconella*

PAPAVER COLORADENSE (Fedde) Fedde ex Woot. & Standley, Contr. U.S. Natl. Herb. 19: 262. 1915. *Papaper nudicaule* subsp. *radicatum* var. *coloradense* Fedde, Repert. Sp. Nov. Regni 7: 256. 1902. **LECTOTYPE (designated here): USA. Colorado.** East of Middle Park, 1867, *Parry 147* (BM 574948! scan).

Papaver coloradense Fedde. Simultaneously and invalidly published in the prologue of *P. nudicaule* var. *coloradense* as "*P. coloradense* Fedde in sched. U.S. Nat. Herb."

Papaver uintaense S.L. Welsh, Utah Flora, 475. 1987. **TYPE: USA. Utah.** Duchesne Co.: Anderson Pass, flank of Kings Peak, Uinta Mountains 12,450 ft, 15 Jul 1979, *Welsh, Neese, & Atwood 19005* (NY 500070! scan).

Alpine plants in Colorado and Utah, north to southern Montana are morphologically coherent and usually have been treated under the non-North American species *Papaver radicatum.* Alternately, they have been misidentified as *P. kluanense* or as *P. pygmaeum.* From *P. kluanense, P. coloradense* differs in its overall small size, smaller petals (8-13) mm, oblong-obovate to narrowly obovate capsules, greener leaves, and smaller, deeper yellow petals.

Like *Papaver pygmaeum*, plants of *P. coloradense* are distinctive among North American boreo-temperate *Papaver* in their small size, comparatively dark green leaves, more persistent petiole bases, rather richly coloured petals, and oblong-obovate to narrowly obovate capsules. In these regards, they differ from *P. kluanense.* I have verified leaf and petal colour by examining field photographs in (for example) Utah TES Plant Interagency Committee (1991) and Colorado Natural Heritage Program (2013). The leaf lobes of *P. coloradense* are often notched or secondarily lobed, but the majority of lobes are entire. By contrast, *P. pygmaeum* has obovate to suborbicular leaf lobes (oblong to oblong-oblanceolate in *P. coloradense*), the leaf lobes are more crowded and more often secondarily lobed, the petals tend to be orange and smaller (5–10 mm), and the capsules have thicker, entirely ivory-white hairs (brown or brown-tipped hairs in *P. coloradense*). Also the two species are geographically separated. *Papaver pygmaeum* reaches its southern extent in northwest Montana ca. 375 km north of the northernmost population of *P. coloradense*, which occurs in the Crazy Mountains in south-central Montana.

Other specimens studied. **USA**. **Colorado**. Gunnison Co.: Gothic, Rocky Mountain Biological Laboratory, White Mountain and Queen Basin, 12900-13200 feet, 13 Jul 2013, *Williams 963* (IDS 64374! scan). Park Co.: E face of Mt. Silverheels on steep ridge slope, Mosquito Range, Pike National Forest, 26 Jul 1991, *Kelso 91-60* (ALA 108461! scan). **Montana**. Carbon Co.: Beartooth Mountains, W-facing slope below Sundance Pass, 15 Aug 1981, *Lesica 1791* (MONT 67914! scan); Beartooth Mountains, NE-facing slope of Silver Run Peak, ca. 15 mi W of Red Lodge, 11 Aug 1987, *Lesica 4490* (MONTU 108440! scan). Park Co.: Crazy Mountain Range, ridge between Crazy Peak and Eddings Peak, 10,800 feet, 28 Jul 1996, *Luna MONTU-1996-6* (MONTU 120374! scan). **Utah**. Duchesne Co.: S of Kings Peak, Ashley National Forest, Uinta Mountains, head of Yellowstone drainage, 21 Aug 1991, *Atwood 16751* (ID 107080! scan); Ashley National

Forest, Uinta Mountains, pass below Wilson Peak, Garfield Basin, 22 Aug 1991, *Atwood 16774* (ID 107065 scan).

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ABELIA (CAPRIFOLIACEAE) IN THE ARKANSAS FLORA

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ABSTRACT

Abelia × *grandiflora* is reported here as occurring outside of cultivation in Arkansas. Escaped plants are documented from three counties: Conway, Garland, and Pulaski. The Garland County plants could possibly have been persistent from cultivation, although they appeared escaped. Photographs of the *Abelia* voucher specimens are provided, along with notes on *Abelia* and the morphologically similar species *Kolkwitzia amabilis*, in Arkansas.

Three records of escaped plants (one possibly long-persistent from cultivation) of *Abelia* × *grandiflora* (Rovelli ex André) Rehd. (glossy abelia) are documented from Conway, Garland, and Pulaski counties (Figs. 2–4) in Arkansas. This taxon has not previously been documented from outside of cultivation in the state (Arkansas Vascular Flora Committee 2006; Gentry et al. 2013). This also is the first documented occurrence of the genus *Abelia* in the Arkansas flora.

Voucher specimens. **Arkansas.** Conway Co.: Along Cedar Creek, T6N, R18W, NW portion of S33, 1 Nov 1986, *Watson 1091* (HEND). Garland Co.: Hot Springs National Park, off Sleepy Valley Rd. immediately E of intersection of Sleepy Valley Rd. and Gulpha Gorge Rd., a few, large plants persisting from prior cultivation, highly disturbed habitat of old residential area being reclaimed by the National Park Service, plants with flowers, many persistent and naturalized exotics, 18 Jul 2017, *Serviss 8578A* (HEND); N of Magnet Cove, edge of county, pine-oak forest, N side of Spanish Mountain, T2S, R17W, S34, a few plants, possibly persisting from cultivation but appeared escaped, no houses in the vicinity, many exotics, 5 Aug 2006, *Peck 06-115* (HEND). Pulaski Co.: Vicinity of Henderson Junior High, weedy greenbelt area behind school, near drainage ditch, 14 Sep 1990, *Schosser 9044* (HEND).

Abelia × *grandiflora* is a semi-evergreen shrub to 2.5 m tall, of interspecific hybrid origin between *A. chinensis* R. Brown and *A. uniflora* R. Brown (Bailey & Bailey 1976; Krüssmann 1976; Rehder 1990; Yang et al. 2011; Fig. 1A–E). It is grown for its showy, usually fragrant flowers and attractive, arching growth form. *Abelia* × *grandiflora* frequently is cultivated in the southern USA, including Arkansas, and previously has been reported as a component of the naturalized floras of Alabama, Arizona, Florida, Georgia, Mississippi, North Carolina, and Texas (Diamond & Woods 2009; Wunderlin & Hansen 2011; Poindexter 2013; Kartesz 2015; Weakley 2015; Keener et al. 2018; USDA, NRCS 2018).

Apparently, under natural conditions, *Abelia* species generally do not establish populations via vegetative/clonal growth and viable seed production is typically low (Landrein et al. 2017), which also has been the observation (of the authors) with Arkansas material. The origin of the escaped *Abelia* plants in Arkansas is unknown; however, establishment from horticultural discards, or possibly from seeds, seems plausible — in the horticultural trade, *Abelia* is commonly propagated through stem cuttings, and adventitious rooting of stem discards could give rise to escaped plants. Because of

its apparent limited ability to establish naturalized populations in the southern USA (Weakley 2015) and long-time and frequent use in landscaping, persistence from cultivation cannot unequivocally be excluded as the origin of at least some of the Arkansas plants. In Arkansas (*Serviss 8578A*) and elsewhere, *A.* × *grandiflora* sometimes is observed as persistent from cultivation but with the appearance of naturalization. The site for the Garland County specimen (*Peck 06-115*) at one time had a house in the vicinity, but it burned down during the 1930s. No other houses are present near the site. Plants at this location could have been persisting from cultivation but appearing as escaped. *A.* × *grandiflora* plants from the sites in Conway and Pulaski counties apparently were present as escapes—the source of their origin, however, is unknown.

Much natural and horticultural variation, produced through a combination of hybridization and introgression among taxa, exists within the genus *Abelia* (Landrein et al. 2017). Taxa of *Abelia* are often difficult to identify and species boundaries, at least in certain instances, are blurred (Landrein et al. 2017). A number of horticultural varieties and forms exist for *A.* × *grandiflora*, and this taxon has been used repetitively in hybridization and introgression with other *Abelia* species to produce a variety of additional cultivars (Krüssmann 1976; Yang et al. 2011; Landrein et al. 2017). The literature indicates that *A.* × *grandiflora* is of hybrid origin between *A. chinensis* and *A. uniflora*; however, molecular studies conducted by Landrein et al. (2017) indicate the parental taxa of *A.* × *grandiflora* are equivocal, with *A. macrotera* (Graebn. and Buchw.) Rehd., rather than *A. chinensis*, the other possible parental taxon (*A. macrotera* × *A. uniflora*) for this hybrid. As a result, precise

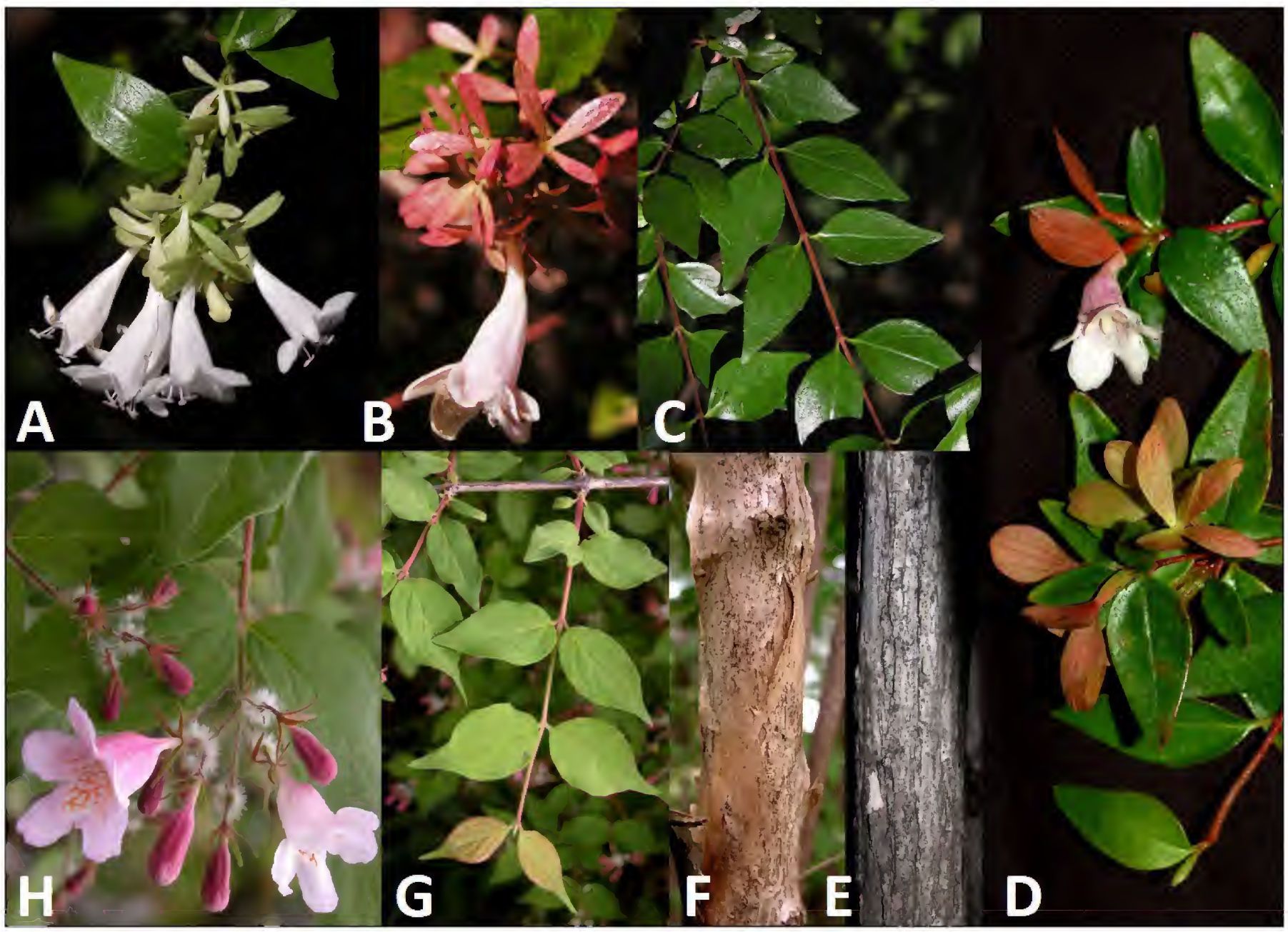

Figure 1. *Abelia* × *grandiflora* and *Kolkwitzia amabilis* for comparison (from cultivated plants in Arkansas). (A-E) *Abelia* × *grandiflora*: (A-B) Flowers (notice the red-colored sepals on Fig. B, which is typical post-anthesis). (C) Leaves and stem. (D) Plant with somewhat wider sepals than those shown in Figs. A and B (photo credit: Renn Tumlison). (E) Mature bark. (F-H) *Kolkwitzia amabilis*: (F) Mature bark. (G) Leaves and stem. (H) Flowers (notice the conspicuous, bristly-hirsute trichomes on the pedicels and ovaries).

Figure 2. Voucher specimen of *Abelia* × *grandiflora* from Conway Co., Arkansas (photo credit: Heather May). The plant was present as an escape along Cedar Creek. Notice the wide corollas, seemingly wider than observed for some *A.* × *grandiflora*, including the specimens from Garland and Pulaski counties. The sepals, which are more typical for *A.* × *grandiflora*, are narrowly lanceolate to oblong, and variable in number, from 2–5 per flower.

Figure 3. Voucher specimen of *Abelia x grandiflora* from Garland Co., Arkansas (photo credit: Heather May). Plants apparently were escaped at this site, or if persistent from cultivation, had the appearance of naturalization. Although the specimen only has a few flowers present, each flower has only two sepals that are elliptic in shape.

Figure 4. Voucher specimen of *Abelia x grandiflora* from Pulaski Co., Arkansas (photo credit: Heather May). The plant was present in an urban greenbelt in Little Rock.

identification of cultivated or escaped plants of *Abelia* may be difficult. The plants documented here appear to fit reasonably well within the morphological boundaries of *A. x grandiflora*.

The *Abelia x grandiflora* specimen from Conway County (Fig. 2) has large flowers (corollas 20-21 mm long and nearly as wide, with some pink coloration, but with the typically narrow sepals that vary in number from 2 to 5 per flower. The Garland County specimen (Fig. 3) appears to fall within the range of characteristics for *A. x grandiflora*, but the flowers have only two sepals, which are elliptic in shape and wider than the lanceolate to oblong sepals often present on specimens of *A. x grandiflora*. Similar plants to the Garland County specimen are cultivated on the Henderson campus and possess elliptic sepals that number from 2 (most common condition) to 4 per flower on the same plant.

Kolkwitzia amabilis Graebn. (beauty bush) is morphologically similar to *Abelia x grandiflora* (see comparisons in Fig. 1). It is a deciduous shrub to 2.5 m tall, native to China (Bailey & Bailey 1976; Krüssmann 1976; Yang et al. 2011) and also cultivated in Arkansas (Fig. 1F–H). It has been observed in Arkansas by the authors (and others) as persistent from cultivation, appearing as possibly escaped (*Serviss 8565*, HEND; *Baker 10-0056*, ANHC, HEND). Although not currently known outside of cultivation in Arkansas, *K. amabilis* has been documented from the naturalized floras of a number of other states (Kartesz 2015; Weakley 2015; USDA, NRCS 2018). A key to the two species is provided here.

1. Flowers with corolla white to pinkish-white, sepals 2–5 per flower, even on same plant; pedicels, ovaries, and fruits glabrous to pubescent but not densely bristly-hirsute; leaves pubescent only on the abaxial (lower) surface ..... **Abelia x grandiflora**
1. Flowers with corolla pale to dark pink, sepals 5; pedicels, ovaries, and fruits densely bristly-hirsute; leaves pubescent on both surfaces ..... **Kolkwitzia amabilis**

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SEVEN NEW STATE RECORDS AND FOUR COUNTY RECORDS FOR THE ARKANSAS FERN FLORA

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ABSTRACT

Seven pteridophyte taxa are reported for the first time as naturalized members of the Arkansas flora: *Arachniodes adiantiformis*, *Asplenium daucifolium*, *Pteris ensiformis* var. *ensiformis*, *Pteris ensiformis* cv. '*evergemiensis*', *Selaginella erythropus* var. *erythropus*, *Selaginella erythropus* cv. '*sanguinea*', and *Selaginella ludoviciana*. Significant county records are reported for four pteridophyte taxa: *Equisetum arvense*, *Nephrolepis exaltata*, *Psilotum nudum*, and *Salvinia molesta*.

The Arkansas fern flora previously was reported as comprising 123 taxa (species, infraspecific taxa, and hybrids), including 98 native and 25 naturalized taxa (Peck 2011a; Peck 2011b). One additional fern species, *Pellaea wrightiana* (Wright's Cliff-brake), was reported as new to Arkansas in 2013 (Witsell 2013). *Pellaea wrightiana* is native to the western USA and ranges from Arizona, southwestern Utah, and Colorado eastward to west Oklahoma and west Texas, but with long-range disjunctive populations farther east in North Carolina, South Carolina, and Virginia. The Arkansas occurrence of *P. wrightiana* is an isolated and disjunct population in novaculite glades in the Jack Mountains south of Hot Springs (Witsell 2013).

The large number of fern escapes from cultivation documented in Arkansas reflects a state-wide interest in the garden cultivation of native and non-native hardy ferns (Crank & Peck 2011). The present report documents continued efforts to locate and record fern escapes in the vicinity of the cities of Little Rock (Pulaski County) and Hot Springs (Garland County).

Seven more taxa are documented here as occurring in Arkansas. Thus, a total of 131 taxa are now known to comprise the Arkansas fern flora, with 100 native and 31 non-native taxa. Pulaski County, in the center of the state, has a known fern flora of 73 taxa, second greatest in Arkansas behind the 82 from Garland County.

New state records

Arachniodes adiantiformis (G. Forest) Tindale (Leather Fern, Florist Fern), Dryopteridaceae.

Introduced to USA, native to and widespread in the Australia, South Africa, and New Zealand (Jones 1987) and extensively cultivated in Florida; escaped from cultivation in Arkansas. This species also is known as *Rumohria adiantiformis* (G. Forest) Ching in the horticultural trade.

Voucher specimens. **Arkansas**. Pulaski Co.: Ivesville section of City of Little Rock, along a creek meander with bamboo thicket, clay soils, escaped from cultivation without an obvious source plant nearby, two large clones from spreading rhizomes, 21 Aug 2011, *Peck 2011570, 2011571* (BRIT).

Asplenium daucifolium Lam. (Mauritius Spleenwort, Mother Fern), Aspleniaceae.

Introduced to USA, native to Mauritius and Madagascar (Jones 1987; Bailey & Bailey 1976); an escape from cultivation in Arkansas. This species sometimes is sold in the horticultural trade under the name of *Asplenium bulbiferum* G. Forest. Two distinct, naturalized populations are reported from Arkansas.

Voucher specimens. **Arkansas**. Pulaski Co.: Ivesville section of City of Little Rock, creek meander along Arkansas 10, with bamboo thicket, clay soils, and escape from cultivation without obvious source plants nearby, two large clones, spreading by rhizomes, 13 Aug 2011, *Peck 2011540, 2011541* (BRIT); Murray City Park, along wooded bluffs overlooking Arkansas River, with normal spores of fertile species, 16 Jun 2012, *Peck 2012100* (BRIT).

Pteris ensiformis Burm. var. **ensiformis** (Slender Brake), Pteridaceae.

Introduced to USA, native to Asia and Australia and widespread in China, India, Japan, Malaysia, Polynesia, and Sri Lanka (Jones 1987; Bailey & Bailey 1976); escaped from cultivation in Arkansas. This species morphologically is similar in appearance to *Pteris cretica* L.

Voucher specimen. **Arkansas**. Pulaski Co.: Ivesville section of City of Little Rock, along Arkansas 10, a creek meander with bamboo thicket, clay soils, an escape from cultivation without obvious source plants nearby, two plants, 3 Aug 2011, *Peck 2011511* (BRIT).

Pteris ensiformis Burm. cv. '**evergemiensis**' (Silver-lace Brake), Pteridaceae.

Introduced to USA; escaped from cultivation in Arkansas. This cultivar of *P. ensiformis* morphologically is similar in appearance to *Pteris cretica* L. var. *albolineata* Hooker.

Voucher specimen. **Arkansas**. Pulaski Co.: Ivesville section of City of Little Rock, along Arkansas 10, a creek meander with bamboo thicket, clay soils, an escape from cultivation without obvious source plants nearby, two plants, 3 Aug 2011, *Peck 2011510* (BRIT).

Selaginella erythropus (Mart.) Spring var. **erythropus** (Red Spikemoss), Selaginellaceae.

Introduced to USA, native to tropical America (Bailey & Bailey 1976); escaped from cultivation in Arkansas.

Voucher specimen. **Arkansas**. Pulaski Co.: Ivesville section of City of Little Rock, along Arkansas 10, a creek meander with bamboo thicket, clay soils, an escape from cultivation without obvious source plants nearby, scattered plants, Sep 2011, *Peck 2011590* (BRIT).

Selaginella erythropus (Mart.) Spring cv. '**sanguinea**' (Ruby Red Spikemoss), Selaginellaceae.

Introduced to USA; escaped from cultivation in Arkansas.

Voucher specimen. **Arkansas**. Pulaski Co.: Ivesville section of City of Little Rock, along Arkansas 10, a creek meander with bamboo thicket, clay soils, an escape from cultivation without obvious source plants nearby, scattered plants, Sep 2011, *Peck 2011591* (BRIT).

Selaginella ludoviciana (A. Braun) A. Braun (Gulf Spike-moss), Selaginellaceae.

This species is native to the southeastern USA, ranging from Florida to Louisiana (Lellinger 1985).

Voucher specimen. **Arkansas**. Pulaski Co.: Moist spoils adjacent to bald cypress swamp along Arkansas River, upstream of Murray Lock and Dam, scattered plants, N side of river on clay bank with seepage moisture, 6 Jun 2011, *Peck 2012101* (BRIT).

Significant county records

Equisetum arvense L. (Field Horsetail), Equisetaceae.

Native to and widespread over much of Canada and USA (Lellinger 1985), including Arkansas. *Equisetum arvense* previously was documented in Arkansas from several northern counties, with Hot Spring County the closest occurrence to the Pulaski County record (Gentry et al. 2013; Peck 2011a).

Voucher specimen. **Arkansas**. Pulaski Co.: Sand spoils along Arkansas River, in forested area along N side of River, above Murray Lock and Dam, scattered plants, 26 Aug 2011, *Peck 2011605* (BRIT).

Nephrolepis exaltata (L.) Schott (Sword Fern), Lomariopsidaceae, Nephrolepidaceae.

Native to the USA, specifically southern and peninsular Florida (Lellinger 1985) but escaping from cultivation in Arkansas. *Nephrolepis exaltata* previously has been documented in Arkansas only from Jefferson County (Gentry et al. 2013; Peck 2011a). The Pulaski County record is the second documented occurrence outside of cultivation.

Voucher specimen. **Arkansas**. Pulaski Co.: Sand spoils along Arkansas River in forested area on N side of river upstream from Murray Lock and Dam, floodwater debris and wrack zone, one older plant and adjacent juveniles from runners, 16 Jun 2011, *Peck 2012102* (BRIT).

Psilotum nudum (L.) P. Beauv. (Skeleton Fern, Whisk Fern), Psilotaceae.

Native to southeastern USA, including Arkansas, also disjunct in Arizona (Lellinger 1985) and central and South America. Some urban plants are spread in root balls of shrubs and trees in the horticultural trade in Arkansas. *Psilotum nudum* previously was documented in Arkansas from most southern counties, with Clark County the only county in proximity to the Pulaski County record (Gentry et al. 2013; Peck 2011a).

Voucher specimen. **Arkansas**. Pulaski Co.: Moist spoils adjacent to bald cypress swamp along Arkansas River on N side of river upstream from Murray Lock and Dam, plants on bases of old stumps, 6 Jul 2011, *Peck 2012103* (BRIT).

Salvinia molesta D.S. Mitchell (Giant Water Spangles), Salviniaceae.

Introduced to USA, native to Argentina and Brazil (Jones 1987); escaping from cultivation in Arkansas and possibly spreading to southern Arkansas from naturalized populations in Louisiana and Texas. *Salvinia molesta* previously has been documented in Arkansas only from Miller and Pulaski counties (Peck 2011a). This second naturalized occurrence from Pulaski County marks only the third Arkansas record.

Voucher specimen. **Arkansas**. Union Co.: Beryl Anthony Lower Ouachita WMA, in the backwater above Lock and Dam 6, 26 Sep 2012, *Peck 2012185* (BRIT, HEND).

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CONFIRMATION OF THE CENTRAL APPALACHIAN XERIC SHALE WOODLAND (CHESTNUT OAK/ BEAR OAK/ POVERTY OATGRASS WOODLAND) COMMUNITY IN SOUTH-CENTRAL PENNSYLVANIA

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ABSTRACT

The mid-Appalachian shale barrens are unique woodland and herbaceous plant communities restricted to steep slopes with an exposed shale substrate. These features support a remarkable assemblage of endemic and near-endemic taxa with diverse evolutionary pathways. The United States National Vegetation Classification System categorizes the mid-Appalachian shale barrens into six community types or associations –– the Central Appalachian Xeric Shale Woodland association was documented in Huntingdon Co., Pennsylvania, while conducting shale barren surveys at Raystown Lake. This community type was previously documented only from Maryland and Virginia; it was described as potentially occurring in Pennsylvania but had not been recorded.

Mid-Appalachian shale barrens were identified, delineated, and classified at Raystown Lake, Huntingdon Co., Pennsylvania, from May - September, 2018. The lake is operated by the U.S. Army Corps of Engineers for the primary purposes of flood control, recreation, hydroelectric power, fish and wildlife, and low-flow augmentation for water quality. It is the largest lake located entirely within Pennsylvania, with a maintained pool of approximately 3,358 ha (8,300 acres), surrounded by 8,498 ha (21,000 acres) of managed land (USACE 2018). Raystown Lake is situated within the Ridge and Valley Province, an area of alternating linear ridges and continuous valleys occurring from New York to Alabama (Fig. 1; USEPA 2013). Ridges are underlain by rock strata that have experienced uplift and are resistant to weathering, while valleys are underlain by softer sediments, shale, and limestone that have weathered to a moderately level surface. Shale barrens occur on slopes in this province as woodlands and openings with short-statured trees, and total vegetative cover that is often sparse relative to adjacent areas. The barrens are distributed in Maryland, Virginia, West Virginia, and south-central Pennsylvania where Upper Devonian, Ordovician, and Silurian shales outcrop (Platt 1951; Keener 1983). The shale surface layer of these barrens, combined with other site factors, severely inhibits seedling development, leading to their characteristic open vegetation structure.

Barrens typically occupy south-east to west facing exposures with steep inclines of 20 to 70 degrees (Keener 1983). The porosity of the coarse rock fragments allows water to infiltrate the soil horizons below but maintains a xeric surface layer. Seedlings that do not rapidly establish their roots below the surface layer of rock fragments perish during the summer. The barrens experience high surface temperatures during summer months, often exceeding 55°C for several hours per day, and have been known to reach 63°C (Platt 1951). These temperatures are greater than the tolerance level of most plants.

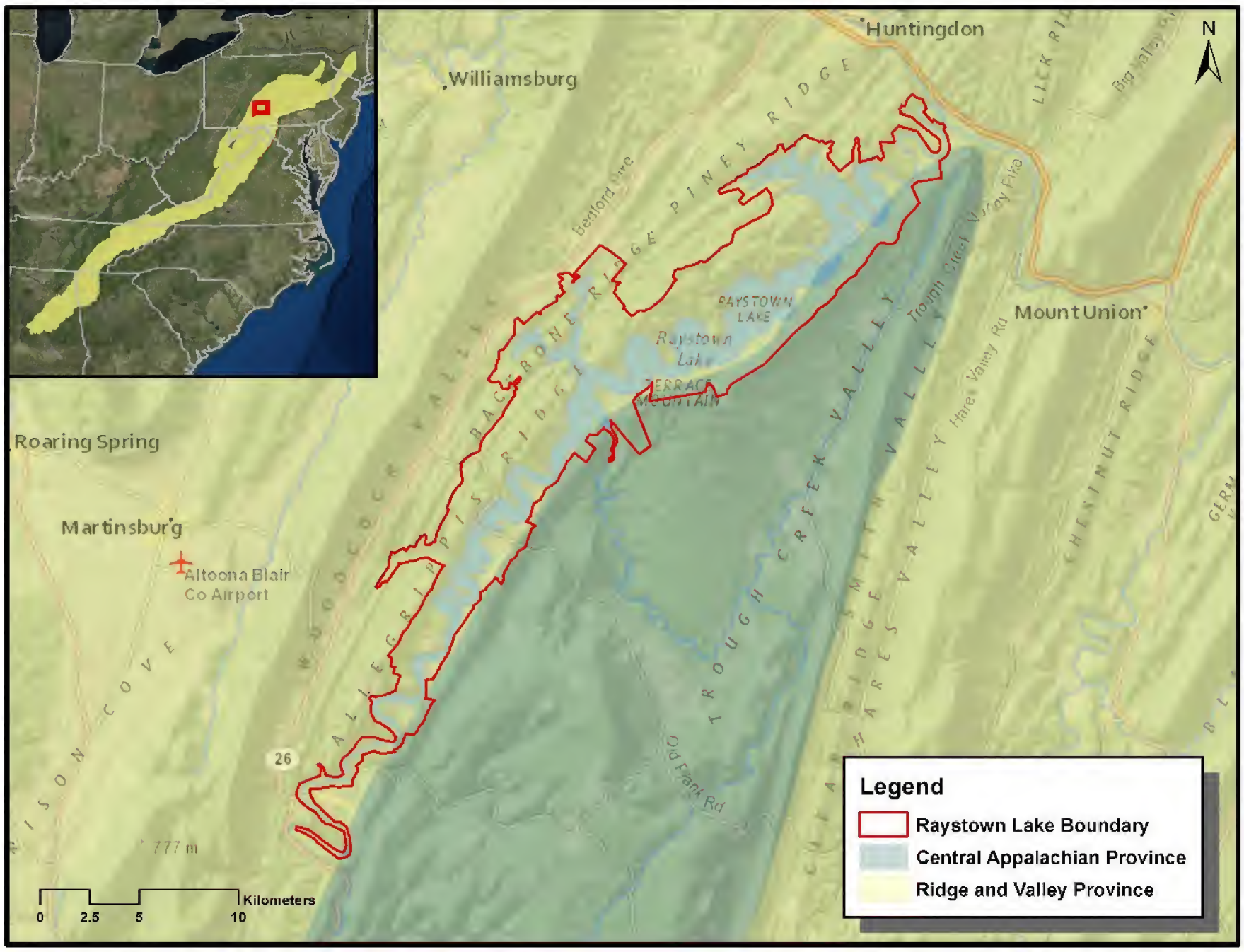

Figure 1. Extent of the Ridge and Valley Province (inset map), and Level III Ecoregions of the Raystown Lake area (USEPA 2013).

The openness of the barrens provides conditions of low competition and high available light in the herbaceous layer. Several plant species are adapted to occupy these features exclusively (shale barren endemic) and are unable to compete in other open habitats such as prairies, fields, and roadsides (Norris & Sullivan 2002). Several other taxa are considered near-endemics, most frequently occurring on shale barrens but also found occupying other suitable open habitats (e.g. rock outcrops, glades; Keener 1983). Seventeen taxa are regarded as shale barren endemics/near-endemics, with eight known to occur in Pennsylvania and tracked by the Pennsylvania Natural Heritage Program (Keener 1983; Weakley 2015; PANHP 2018). The remaining species, in addition to the eight known from Pennsylvania, occur primarily in Virginia and West Virginia.

The National Vegetation Classification System (USNVC 2017) describes two of the six mid-Appalachian shale barren associations as reported in Pennsylvania: the North-Central Appalachian Acidic Shale Woodland and the Central Appalachian Circumneutral Barrens. These associations differ in substrate pH, which leads to differences in species composition and structure. The former is often dominated by *Pinus virginiana* with a sparse understory, while the latter is often dominated by *Juniperus virginiana* with a variable understory of shrubs and herbs (USNVC 2018). The majority of areas delineated as shale barrens at Raystown Lake were classified within these two types; another shale barren association, however, was observed during our survey.

The USNVC (2017) lists the occurrence of the Central Appalachian Xeric Shale Woodland association as "potential" in Pennsylvania, with recorded sites only known from Maryland (6 sample

locations) and Virginia (12 sample locations). This association is also listed as potentially occurring in West Virginia. Select shale barren features and portions of larger features observed at Raystown Lake appeared to fit the description of this community type. Stunted and contorted specimens of *Quercus montana* dominate the overstory of this woodland community, with *Quercus rubra* and *Carya glabra* frequently occurring and occasionally occurring as co-dominants. Conifers such as *Juniperus virginiana* and *Pinus virginiana* were sparse or absent entirely. The shrub *Quercus ilicifolia* is a common component, though typically sparse or occurring as widely scattered patches. Other shrubs include *Rosa carolina* and *Vaccinium pallidum*. In some areas, *Quercus montana* and *Q. rubra* seedlings are the only woody subcanopy species encountered. The herbaceous layer is typically sparse (Fig. 2) but occasionally has significant cover represented by graminoids (Fig. 3). *Carex pensylvanica* and *Danthonia spicata* are frequently the dominant herbs.

Figure 2. *Quercus montana* dominates shale woodlands with sparse understory components, Raystown Lake. Note: What appears as open sky in the bottom photograph is the lake below the steep slope.

Figure 3. Shale woodlands dominated by *Quercus montana*, with a variable understory of graminoids, Raystown Lake.

Survey areas were identified based on estimates of tree canopy cover in aerial photography. Distinct features at Raystown Lake that appeared to have approximately 70 percent or less tree canopy cover were digitized in ArcGIS® for field sampling. Plots were established in a subset of survey areas to describe plant community structure and composition. A 100 m^2 rectangular plot (12.5 m x 8 m) was established in one of these features during the autumn sampling period in September 2018 (Fig. 4). Species composition and structure within the plot is shown in Table 1. Sixteen species were recorded, with *Quercus montana* dominating the tree and shrub strata. The herbaceous stratum was sparse with only eight species recorded, with a total of 16.5% cover.

According to USNVC (2017), the Central Appalachian Xeric Shale Woodland community frequently borders other shale barren vegetation types. This pattern was observed at Raystown Lake, while some areas occurred as inclusions within other shale barren communities. Five features were classified as this association and occupied approximately 4.2 ha (10.3 acres) or 5.1% of the total area categorized as shale barrens (81.0 ha [200.2 acres]). The average area of each feature was 0.8 ha (2.2 acres), with the largest occupying 2.2 ha (5.6 acres). Shale barren endemic/near-endemic species were not observed in this particular community type, but the state-listed *Lathyrus venosus* Muhl. ex Willd. was documented during the study (PANHP 2018).

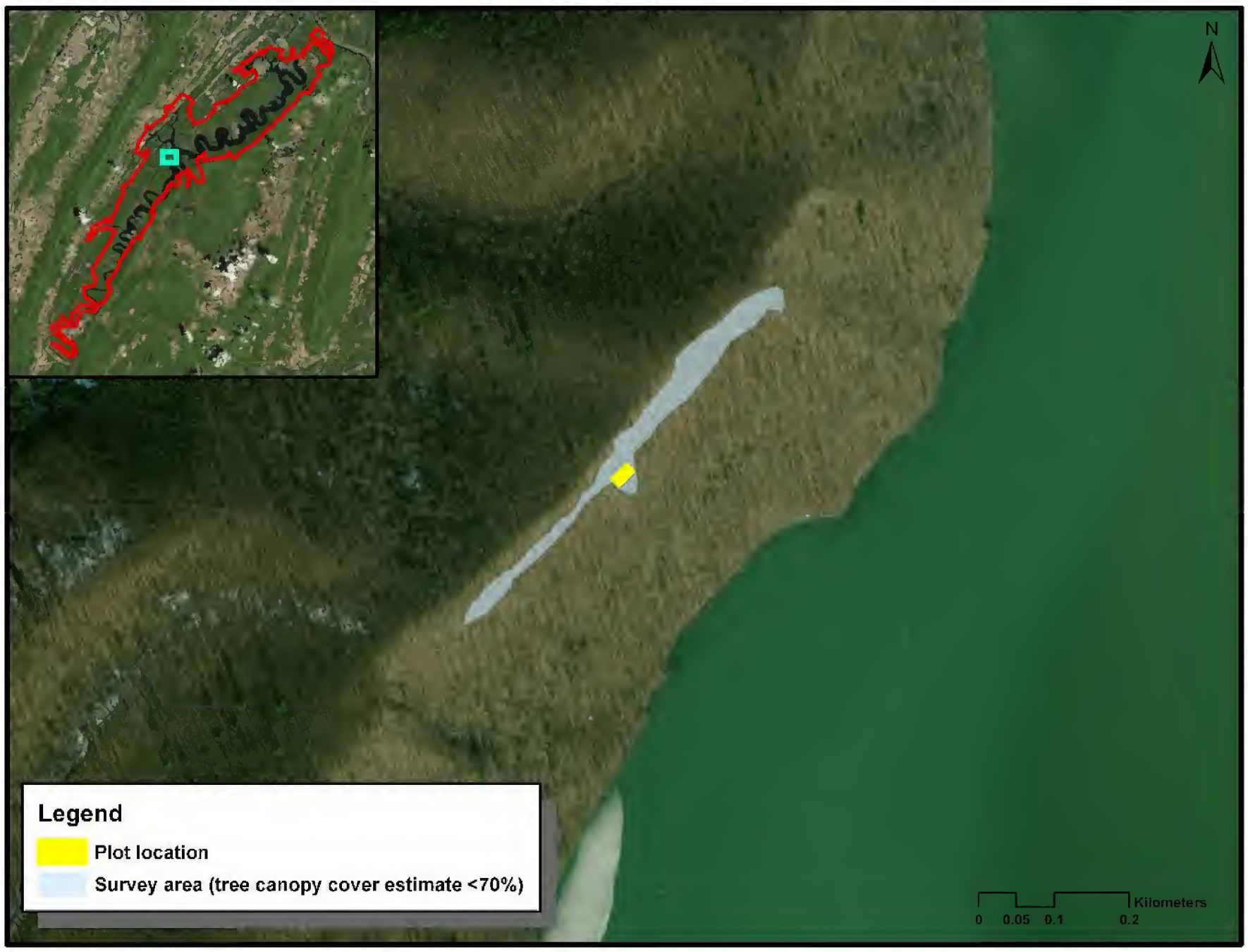

Figure 4. Plot location described as Central Appalachian Xeric Shale Woodland, within a survey area at Raystown Lake.

The relatively small area occupied by features classified as Central Appalachian Xeric Shale Woodlands and their embedded positions within other shale barren communities may lead to overlooking this community. Additionally, the lack of shale barren endemic/near-endemic plant species and sparsely vegetated understory does little to encourage further study. However, these communities may have the potential to support endemic/near-endemic plants and provide suitable habitat for rare invertebrates and therefore are worthy of conservation and further study (PANHP 2018). Understanding the distribution of the various associations that are attributed to the mid-Appalachian shale barrens –– their extent and community composition and structure –– is vital for comprehensive study of this unique, geologically restricted community.

Table 1. Shale barren vegetation structure and composition within a 100 m^2 (12.5 m x 8m) plot, Raystown Lake, PA.

Stratum	Species name	% Cover
Canopy tree	*Quercus montana* Willd.	15
Canopy tree	*Quercus rubra* L.	8
Canopy tree	*Carya glabra* (Mill.) Sweet	5
Canopy tree	*Pinus virginiana* Mill.	1
Shrub >1 m	*Quercus montana* Willd.	5
Shrub >1 m	*Quercus rubra* L.	2
Shrub >1 m	*Quercus velutina* Lam.	1
Shrub >1 m	*Prunus serotina* Ehrh.	1
Shrub <1m	*Pinus virginiana* Mill.	0.5
Shrub <1m	*Ailanthus altissima* (Mill.) Swingle	0.5
Herb	*Hedeoma pulegioides* (L.) Pers.	5
Herb	*Avenella flexuosa* (L.) Drejer	3
Herb	*Carex pensylvanica* Lam.	2
Herb	*Danthonia spicata* (L.) Beauv. ex Roem. & Schult.	2
Herb	*Cunila origanoides* (L.) Britt.	2
Herb	*Erechtites hieraciifolius* (L.) Raf. ex DC.	1
Herb	*Trichostema dichotomum* L.	1
Herb	*Solidago bicolor* L.	0.5
Non-vascular	*Cladonia* sp.	5

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A NEW SPECIES OF *LOMATIUM* (APIACEAE) FROM RED MOUNTAIN, A SERPENTINE ISLAND IN MENDOCINO COUNTY, CALIFORNIA

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ABSTRACT

A *Lomatium* species is endemic to Red Mountain, an ultramafic habitat island in northern Mendocino Co., California. It has been misidentified as three different species, *L. congdonii, L. engelmannii,* and *L. tracyi*, but differs from all of them and is described here as **Lomatium kogholiin**i Mason & Willie, **sp. nov.**, the Wailaki *Lomatium*.

When reviewing *Lomatium* for the Flora of North America project (Flora of North America Editorial Committee 1993-ongoing), we were struck by a series of specimens identified as *L. congdonii* J.M. Coulter & Rose reported from Red Mountain, Mendocino Co., California (Constance & Weatherwax 2017). This location is far from the known range of *L. congdonii,* which grows on ultramafic soils in the western foothills of the Sierra Nevada. *Lomatium* seeds are not well adapted to long-distance dispersal (Marisco & Hellman 2009), so the plants from Red Mountain were unlikely to be *L. congdonii*.

Red Mountain is a massive outcrop of ultramafic rock surrounded by sedimentary and metamorphic bedrock (USGS 2018) within the ancestral territory of the Native American Wailaki tribe. The contrast between the ultramafic mountain and surrounding geologic zones can be detected easily in aerial photos because of visible differences in vegetation density and the striking red color of the ultramafic soils on the mountain (Google LLC 2018). For plants adapted to ultramafic substrates, Red Mountain functions as a habitat island. At least 3 species are previously known to be endemic to

the site, *Arabis macdonaldiana* Eastwood, *Eriogonum kelloggii* A. Gray, and *Sedum eastwoodiae* (Britton) A. Berger (USFWS 2013).

Two *Lomatium* species occur on Red Mountain. One, confirmed by numerous herbarium specimens and our own field work, is *L. dasycarpum* (Torrey & A. Gray) J.M. Coulter & Rose. It is distinguished by its pale, tomentose petals and highly dissected leaves. It is ignored for the remainder of this article, which concentrates on smaller plants with glabrous yellow petals and less divided leaves.

This second *Lomatium* has been identified as *L. engelmannii* Mathias and *L. tracyi* Mathias & Constance, as well as *L. congdonii* (Table 2). All three of these species are similar in size and all grow on ultramafic substrates in central and northern California (Figure 3; Appendix 3). Given the limited area of Red Mountain, it seemed unlikely that more than one of these similar species could be present. More troubling, the plants from Red Mountain seemed to differ somewhat from each of the described species. Because of similarities between these species, we used DNA sequences as well as traditional taxonomic methods to compare them.

Methods – morphology

We examined specimens identified as *Lomatium congdonii*, *L. engelmannii,* and *L. tracyi* from from CAS, HSC, JEPS, ORE, OSC, and UC (herbarium acronyms from Thiers, continually updated; Appendix 1). We also examined high quality scans kept at OSC of *L. engelmannii* specimens located at SOC, and scans of the types of *L. congdonii*, *L. engelmannii,* and *L. tracyi* made available on the websites of the relevant herbaria (Table 1).

Table 1. Links to scans of type specimens of *Lomatium congdonii*, *L. engelmannii,* and *L. tracyi* available on the internet.

Species	Herbarium	URL of type or through which type can be found
L. congdonii	US	https://collections.nmnh.si.edu/search/botany/?ti=3
L. engelmannii	MO	http://www.tropicos.org/ImageSearch.aspx
L. tracyi	UC	https://webapps.cspace.berkeley.edu/ucjeps/imageserver/blobs/c81c2dd0-b160-4e46-8fab/derivatives/OriginalJpeg/content

One of us (KM) travelled through northern California to visit known sites where these three species grow, and two of us (KM and JW) visited Red Mountain to examine the plants. Samples collected from this trip were used for DNA extraction (Appendix 2). Plants were identified using the Jepson Manual (Constance & Mathias 2013, 2017) and by comparison with other labeled, and in many cases annotated, specimens (Appendix 1).

Methods – DNA

DNA was extracted from all samples using a Qiagen DNeasy plant mini kit (Qiagen, Valencia, California), following the manufacturer's instructions with the exception that incubation of the samples at 60°C was extended to 2 hours. Amplification of all regions used the primers and methods of Smith et al. (2018). Successful amplifications were determined by viewing aliquots on 1% agarose gels stained with ethidium bromide and viewed under UV illumination. All successful amplifications were purified using Exo-SAPit (Affymetrix, Cleveland, Ohio) and shipped to GeneWiz (Plainfield, New Jersey) for sequencing of complementary strands. Chromatograms were edited and assembled using Phy-DE (Müller et al. 2010). New samples for this publication are listed in Appendix 2 with GenBank numbers. All other samples were previously published in Smith et al. (2018) and voucher information as well as GenBank numbers for these samples can be found there.

Sequences were aligned for each of the seven regions separately, inserting gaps to maintain homology among characters. Ambiguous portions of the alignments and areas with large stretches of missing data were removed from the ends of all regions. A concatenated dataset for all seven regions was then generated and used as the basis for all phylogenetic analyses.

Maximum parsimony (MP) and MP bootstrap with 1,000 replicates (MPBS) were evaluated using PRAP2 (Müller 2004) in conjunction with PAUP* (Swofford 2002). Maximum likelihood (ML) was assessed using RaxML (Stamatakis, 2006) on the CIPRES Science Gateway (Miller et al. 2010) under the default GTR + G + I model and allowing bootstrapping (MLBS) using one model with joint branch length optimization to stop automatically using the default autoMRE. Consensus trees were generated and viewed in MEGA 7 (Kumar et al. 2016). The best fit model for DNA evolution was determined using jModelTest 2.1.7 (Darriba et al. 2012) and used for the Bayesian analysis (BI) with MrBayes 3.2 (Ronquist et al. 2012). Majority rule consensus trees of the output were generated in PAUP* and effective sample size (ESS) values were estimated in Tracer (Rambaut et al. 2014).

Results – morphology

The Wailaki *Lomatium* and the species most similar to it differed in several traits, including ray number and the size and oil tubes of the fruit (Table 3). Details of how the leaves were divided among species were the most useful traits for distinguishing the taxa but the hardest to communicate (Figs. 2, 4). Sample sizes for traits of mature fruits were limited, because, as is true for most *Lomatium* (KM, BLW pers. obs.), specimens are usually collected in flower or with young fruit.

The trait that most easily distinguishes the Wailaki *Lomatium* from the two similar species that grow in northwest California (*L. engelmannii* and *L. tracyi*) is its lack of bractlets. This is a trait the Wailaki *Lomatium* shares with *L. congdonii*.

Petal color is a useful trait for identifying the Wailaki *Lomatium,* but confusion surrounds the color because in *Lomatium* both yellow and white flowers often dry white or cream-colored. The Wailaki *Lomatium* and *L. congdonii* both have yellow flowers (Fig. 4; KM pers. obs.; CalPhotos continually updated). *Lomatium engelmannii* petals are white (pers. observ.; CalPhotos 2017) or purplish (Constance & Wetherwax 2012, 2017), although they were originally described as "yellow (?)" (Mathias 1938). Petals were originally reported as yellow in *L. tracyi* (Mathias & Constance 1942), based on a series of Tracy specimens collected 1923-1936 in Humboldt and Trinity counties, and they still are reported as yellow (Constance & Wetherwax 2012, 2017). However, the plants we have seen from Trinity County have white petals [KM pers. observ.; Photo 0000 0000 1009 2993 (2009-10-30) posted by J.K. Nelson on Cal Photos]. We are uncertain about the petal color of *L. tracyi* growing in Humboldt County because it usually cannot be judged from dried specimens.

Two CAS specimens labeled *Lomatium tracyi* and collected south of Red Mountain (*Smith 6203* and *Smith & Wheeler 6229A*) turned out to be *L. caruifolium* (Hook. & Arnold) J.M. Coulter & Rose. *Lomatium caruifolium* has yellow flowers and much wider bractlets than *L. tracyi*.

Clarifying the morphology of the similar *Lomatium* of ultramafic habitats also clarified their ranges (Fig. 3). Distances from Red Mountain to the range of *L. congdonii* is 284 km east-southeast, to *L. engelmannii* is 167 km northeast, and to *L. tracyi* is 61 km north. Comparison with a geologic map of California revealed that each taxon (including the Wailaki *Lomatium*) is associated with a different ultramafic bedrock that formed at a different time and has somewhat different components (USGS 2018; Appendix 3).

Table 2. Earlier names given to *Lomatium* herbarium specimens from Red Mountain that have no bractlets, yellow flowers, and little-divided leaves, here described as *L. kogholiini.*

Earlier name	Herb.	Collector	Coll. #	Day	Month	Year
L. congdonii	UC	L. Constance & R. C. Rollins	3003	21	5	1942
L. congdonii	UC	A. Eastwood & J. T. Howell	6131	7	7	1938
L. congdonii	UC	M. E. Mathias & L. Constance	6527			1867
L. congdonii	UC	T. Nelson & J. Nelson	4566	7	4	1979
L. tracyi	CAS	R. Gankin , R. Hildreth, and W. & I. Knight	2719	15	7	1969
L. tracyi	UC	G. F. Hrusa, H. Townsend, & T. Nosall	11884	8	6	1994
L. engelmannii	HSC	T. Nelson & A. Goes	2394	3	5	1976
L. engelmannii	HSC	T. Nelson & A. Goes	2400	3	5	1976
L. engelmannii	HSC	T. Nelson, A. Goes, & J. Nelson	2427	4	5	1976
L. engelmannii	HSC	T. Nelson, A. Goes, & J. Nelson	2434	4	5	1976
L. engelmannii	HSC	T. Nelson & A. Goes	2570	23	5	1976
L. engelmannii	HSC	T. Nelson & A. Goes	2571	23	5	1975
L. engelmannii	HSC	J. Sawyer & T. Nelson	2878	30	4	1977

Table 3. Morphological differences among the *Lomatium* taxa studied. ULS = ultimate leaf segments, the smallest units into which the leaf is divided. Sources: Constance & Weatherwax 2012, 2017, and measurement of herbarium specimens (Appendix 1). ULS = ultimate leaf segment.

	L. kogholiini	***L. congdonii***	***L. engelmannii***	***L. tracyi***
Petal color	yellow	yellow	white or purplish-white	white or yellow?
Bractlets	usually absent	usually absent	present or absent	present
Bractlets, if present	linear to lanceolate	linear to lanceolate	linear, lanceolate, or obovate	obovate or oblanceolate
Leaf color	green	gray-green	blue-green or gray-green, seldom green	green or blue-green
Rays	4–7	6–18	2–12	6–12
Oil ducts on commissure	4–6	2–4	2–6	7
Fruiting Pedicel	3–16 mm	5–12 mm	(2–) 3–9 mm	1–5 (–6) mm
Fruit Length	7.8–10 mm	7–10 mm	7–14 mm	4.8–10 (–11.5) mm
Leaf Surface	glabrous	glabrous or scabrous	glabrous, scabrous, or sparsely puberulent	glabrous
ULS callus tip length	0–0.1 mm	0.1–0.2 mm	0.1–0.2 mm, generally more pointed	0–0.1 mm, generally less pointed
ULS length	0.5–4 (–6.5) mm	3–10 mm	1–3 (–6) mm	0.5–3 (–7) mm

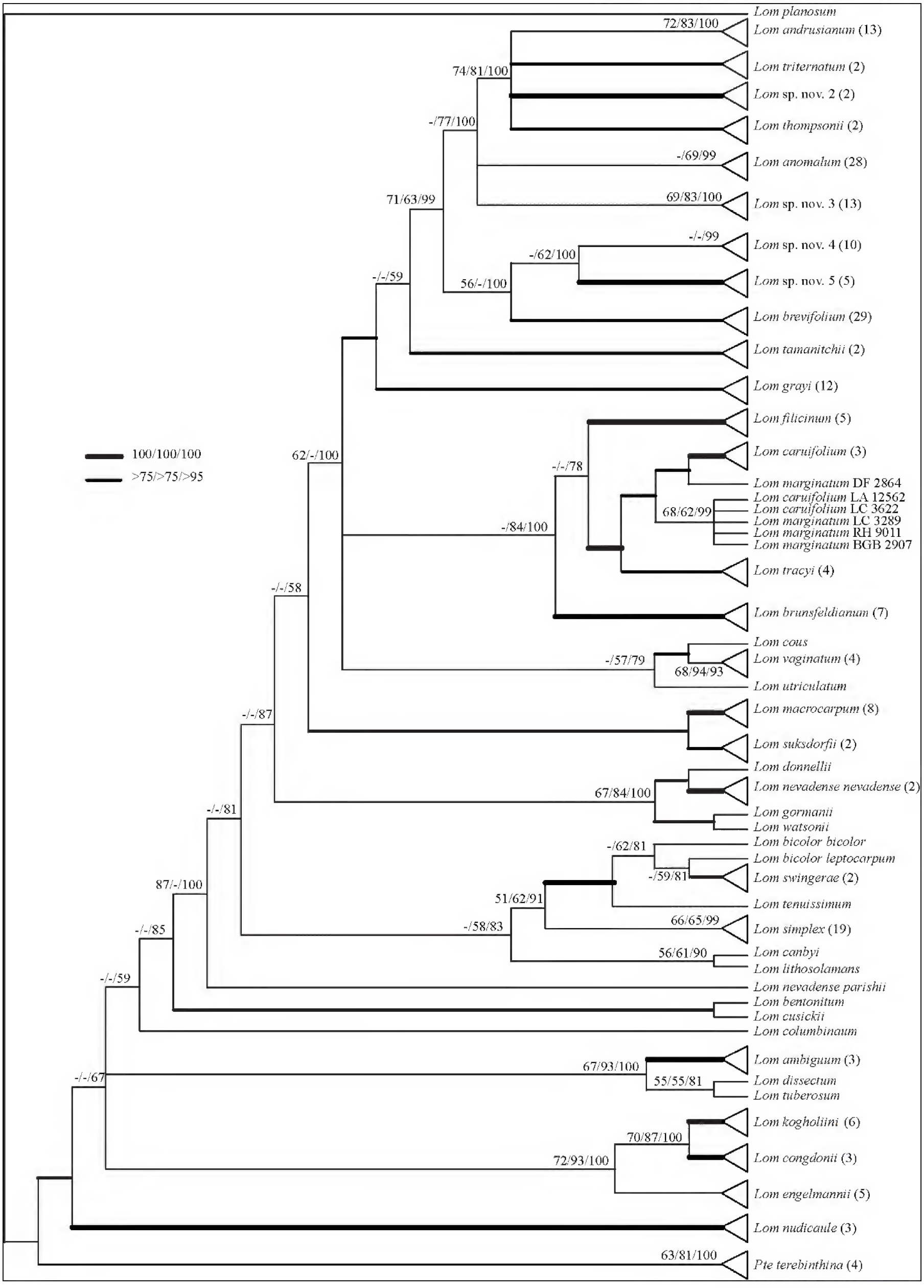
100/100/100
>75/>75/>95
Lom planosum
Lom andrusianum (13)
Lom triternatum (2)
Lom sp. nov. 2 (2)
Lom thompsonii (2)
Lom anomalum (28)
Lom sp. nov. 3 (13)
Lom sp. nov. 4 (10)
Lom sp. nov. 5 (5)
Lom brevifolium (29)
Lom tamanitchii (2)
Lom grayi (12)
Lom filicinum (5)
Lom caruifolium (3)
Lom marginatum DF 2864
Lom caruifolium LA 12562
Lom caruifolium LC 3622
Lom marginatum LC 3289
Lom marginatum RH 9011
Lom marginatum BGB 2907
Lom tracyi (4)
Lom brunsfeldianum (7)
Lom cous
Lom vaginatum (4)
Lom utriculatum
Lom macrocarpum (8)
Lom suksdorfii (2)
Lom donnellii
Lom nevadense nevadense (2)
Lom gormanii
Lom watsonii
Lom bicolor bicolor
Lom bicolor leptocarpum
Lom swingerae (2)
Lom tenuissimum
Lom simplex (19)
Lom canbyi
Lom lithosolamans
Lom nevadense parishii
Lom bentonitum
Lom cusickii
Lom columbinaum
Lom ambiguum (3)
Lom dissectum
Lom tuberosum
Lom kogholiini (6)
Lom congdonii (3)
Lom engelmannii (5)
Lom nudicaule (3)
Pte terebinthina (4)
72/83/100
74/81/100
-/77/100
-/69/99
71/63/99
69/83/100
-/-/99
-/62/100
-/-/59
56/-/100
62/-/100
-/-/78
68/62/99
-/84/100
-/-/58
-/57/79
68/94/93
-/-/87
67/84/100
-/-/81
-/62/81
-/59/81
87/-/100
51/62/91
-/-/85
-/58/83
66/65/99
56/61/90
-/-/59
-/-/67
67/93/100
55/55/81
70/87/100
72/93/100
63/81/100

Figure 1. Majority-rule consensus tree from Bayesian inference analysis with maximum parsimony and maximum likelihood support on corresponding branches. Numbers above branches are maximum parsimony bootstrap/maximum likelihood bootstrap/Bayesian inference posterior probabilities. A dash indicates bootstrap support less than 50. Maximal support from all three analyses are indicated with branches of triple thickness, and support that was greater or equal to 75 for both bootstrap values and greater or equal to 95 posterior probabilities are shown with branches of double thickness. Lom = *Lomatium,* Pte = *Pteryxia.* Letters and numbers following taxon names indicate individuals that are cited in Appendix 2. Where species are recovered as monophyletic, the clades are collapsed and the number of species sampled in each clade is indicated in parentheses following the name

Results – DNA

Amplifications were successful for nearly all regions and all samples, but some of the herbarium material did not amplify for all regions (Appendix 2). The three methods of phylogenetic analyses were congruent with each other, with the greatest resolution from the BI analyses. The two separate runs of the BI analyses were fully congruent and posterior probability support differed between the two by only a single point. The majority rule consensus of the BI trees is presented in Fig. 1 with MPBS and MLBS mapped onto the tree where clades were the same. Maximum parsimony resulted in 199 most-parsimonious trees (length = 2704 steps, consistency index (CI) excluding uninformative positions = 0.4473, retention index (RI) = 0.8467, rescaled consistency index (RC) = 0.4625). The TVM + I + G model was selected by jModelTest and implemented in the BI analyses. The ESS values were 1717.6 and 1,833.8 for the two runs.

Two clusters of taxa are relevant to this study (Fig. 1). One consists of *Lomatium caruifolium, L. marginatum,* and *L. tracyi*. The other consists of *L. engelmannii, L. congdonii,* and the Wailaki *Lomatium*.

Discussion

We initially hypothesized that the Wailaki *Lomatium* from Red Mountain was closely related to *L. tracyi* because Red Mountain is within what was reported to be the range of *L. tracyi,* and the Wailaki *Lomatium* has yellow petals, as *L. tracyi* was reported to have (Mathias & Constance 1942, 1944-1945; Constance & Weatherwax 2012, 2017). However, our hypothesis was false for several reasons. First, Red Mountain is not within the range of *L. tracyi*; *L. tracyi* specimens reported from south of Red Mountain are *L. caruifolium*. Second, *L. tracyi* in Trinity County has white to purplish petals and cream to purple anthers (K Mason 137, 138, and 146; Appendix 1, specimens examined). We have not yet found strong evidence about the fresh petal color of Humboldt County populations of *L. tracyi*. Most important, an analysis of DNA sequences indicates that *L. tracyi* is related to *L. caruifolium* and *L. marginatum,* not the plants from Red Mountain and its relatives (Fig. 1). A Humboldt County specimen of *L. tracyi* (*Chambers 5517*) was included in the study. Whatever its petal color, it clustered with the other *L. tracyi,* not with the Wailaki *Lomatium* (Fig. 1). The Wailaki *Lomatium* also differs from *Lomatium tracyi* in ultimate leaf segments shape, bractlet presence and (when present) shape, leaf color, and other morphologic characters (Table 3).

The Wailaki *Lomatium* is morphologically and genetically similar to *L. congdonii*. Both lack bractlets and have yellow petals and relatively long fruiting pedicels. They differ in several traits including number of rays, ultimate leaf segment length, and the size and oil ducts of the fruit (Table 3), but molecular data indicate that they are sister taxa (Figure 1). The Wailaki *Lomatium* is relatively geographically separated from *L. engelmannii* and differs from it in petal color and bractlet presence (Table 3). However, its leaves are more similar to those of *L. engelmannii* than those of *L. tracyi.* We conclude that the *Lomatium* plants from Red Mountain are distinct from *L. congdonii, L. engelmannii,* and *L. tracyi* and describe it as a species, *L. kogholiini*.

LOMATIUM KOGHOLIINI K.M. Mason & E. Willie, **sp. nov**. **TYPE: California**. Mendocino Co.: Red Mountain summit, 1222 m, 8 May 2018, *K.M. Mason & Wheeler 121* (holotype: OSC; isotypes: CAS, HSC).

Similar to *Lomatium congdonii* but with fewer rays and more oil ducts on commissure; similar to *L. engelmannii* but petals yellow and bractlets absent.

Herbs 0.5–3.8 dm, acaulous, glabrous, green; taproot slender; caudex simple, with basal sheaths of previous years present or absent, with or without persistent peduncles; pseudoscape absent. **Leaves** green, glabrous; basal leaves with petioles 50–150% as long as blades, partially or wholly sheathing; blades broadly ovate to triangular, 3–15 × 2.2–16 cm; ultimate leaf segments 80–400, elliptic to lanceolate, 0.5–4(–6.5) × 0.5–1 mm, entire, acute, apiculate, with calluses 0–0.1 mm. **Peduncles** 1–2 per plant, 4.5–28 cm, exceeding leaves, 0.5–1.8 mm wide 1 cm below apex, decumbent, ascending, or erect, not inflated, glabrous. **Umbels**: 2.2–3.4 cm wide in flower, 2.5–6(–10.5) cm wide in fruit; rays 4–7, 2–5 of them fertile, 0.5–3(–13.2) cm long in fruit, glabrous, unequal, ascending to spreading; involucel usually absent, if present not dimidiate; bractlets 0(-2), if present usually vestigial, linear to lanceolate, 1.5–5 mm, shorter than flowers, glabrous, distinct, margins narrowly scarious, not ciliate, entire. **Pedicels** 3–16 mm in fruit, shorter or longer than the fruit. **Flowers:** petals yellow, glabrous; anthers yellow; ovary and fruit glabrous. **Mericarps** dorsiventrally compressed, broadly oblong, 7.8–10 × 3.5–5 mm, length/width ratio 1.8–2.2, obtuse to rounded; wings 0.5–1.3 mm wide, 28–52% of body width, paler than body; dorsal ribs slightly or not raised; oil ducts 1 in intervals, 4–6 on commissure, conspicuous. **Chromosome number**, *n*=11, (note on *Nelson & Nelson 4566* from UC). Figures 2 and 4.

Flowering early April–June, fruiting June–July. Open jeffrey pine (*Pinus jeffreyi*) plant communities with sugar pine (*Pinus lambertiana*), on serpentine soil, elevation 400–1250 m, characteristically with *Pinus attenuata, Calocedrus decurrens, Arctostaphylos manzanita, Ceanothus pumilus, Quercus vaccinifolia, Allium falcifolium Pedicularis densiflora,* and *Sedum eastwoodiae*. Endemic to Wailaki Territory, specifically Red Mountain and Little Red Mountain of Mendocino Co., California, north of Cummings.

"Kogholiini" (accent on the first i; *kog-oh-LI-in-ee*) is Wailaki for "daylight coming." The plant was found on Wailaki ancestral land. The Wailaki name was chosen to honor the connection between the plant and the Wailaki people, a name worthy of the special standing of *Lomatium* in the herbal and native worlds. The phrase was found in the lyrics of an old traditional female puberty song.

Other collections examined. USA. California. Mendocino Co.: Summmit, "Big" Red Mountain, 5 mi SE of Bell Springs, 4000 ft, 21 May 1942, *Constance & Rollins 3003* (UC); near Cummings P. O., 7 Jul 1938, *Eastwood & Howell 6131* (UC); Red Mountain, 3400 ft, 15 Jul 1969, *Gankin et al. 2719* (CAS); on summit, 1250 m, 8 Jun 1994, *Hrusa et al. 11884* (UC); Red Mtns., 1867, *Mathias & Constance 6527* (UC); along road on E side of Red Mountain, 3800 ft, 3 May 1976, *Nelson & Goes 2394* (HSC); E of road along E side of Red Mountain, 4000 ft, 3 May 1976, *Nelson & Goes 2400* (HSC); at S end of BLM road to School Section Creek, just above creek, 2800 ft, 4 May 1976, *Nelson et al. 2427* (HSC); along ridge beween the forks of School Section Creek, 3200 ft, 4 May 1976, *Nelson et al. 2434* (HSC); along road to Little Red Mountain, 2700 ft, 23 May 1976, *Nelson et al. 2570* (HSC); along road to Little Red Mountain, 2700 ft, 23 May 1975, *Nelson & Goes 2571* (HSC); at S end of BLM road to Red Mountain, across School Section Creek from end of road, 2800 ft, 7 Apr 1979, *Nelson & Nelson 4566* (UC); Cedar Spring Road to Red Mountain, 3400 ft, 30 Apr 1977, *Sawyer & Nelson 2878* (HSC).

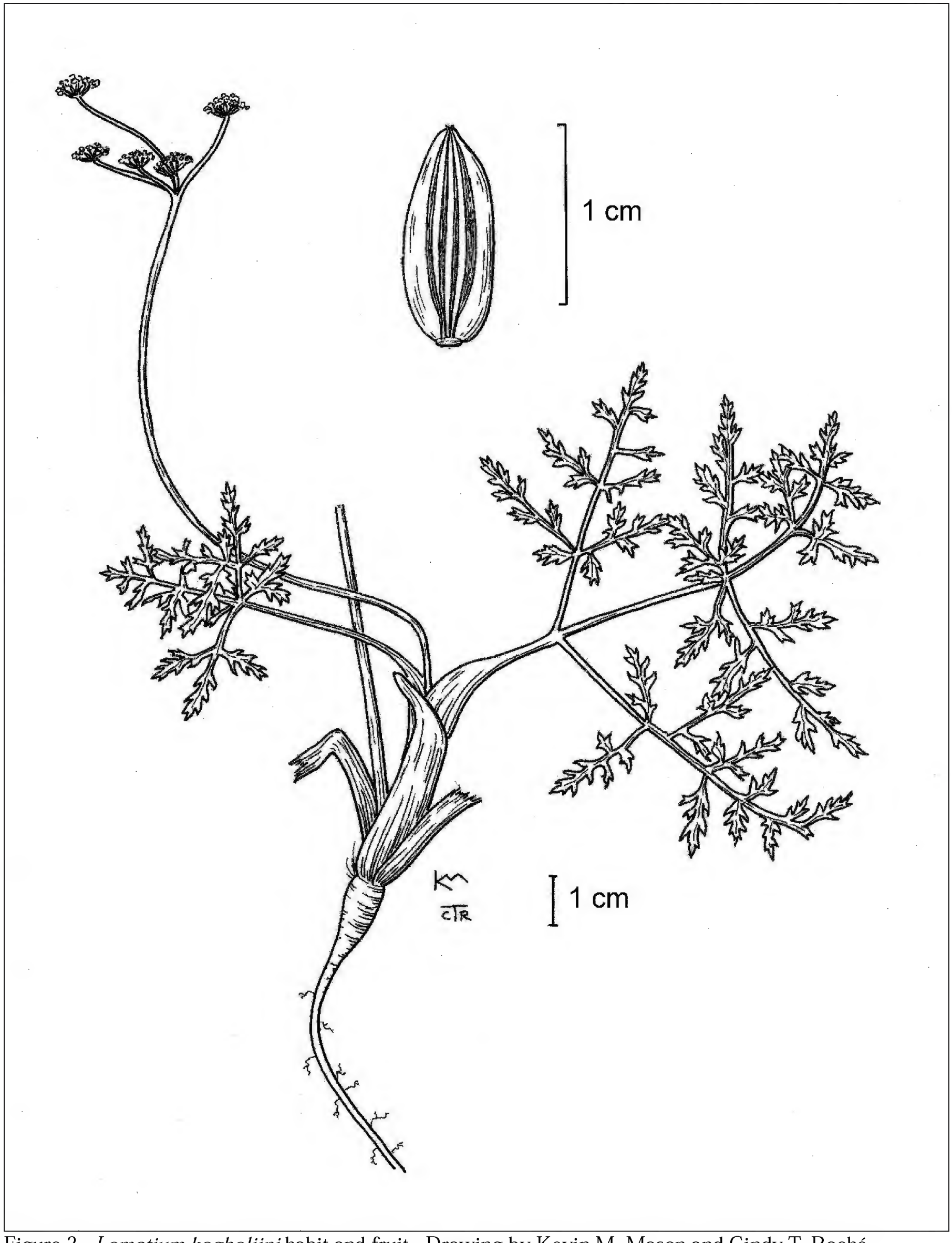

Figure 2. *Lomatium kogholiini* habit and fruit. Drawing by Kevin M. Mason and Cindy T. Roché.

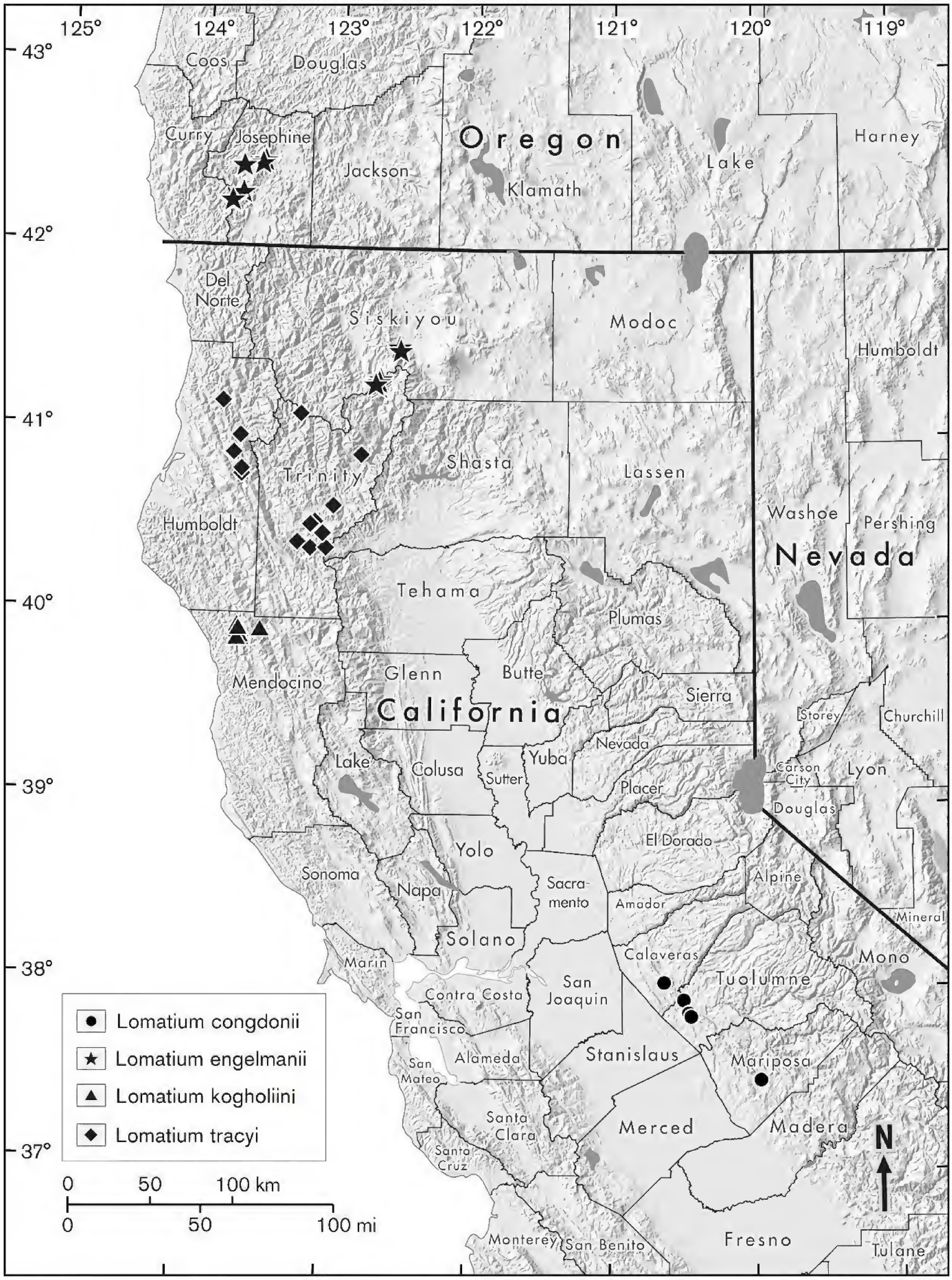

Figure 3. Distribution of *Lomatium kogholiini* and similar species.

Figure 4. Morphological variation in flowering *Lomatium kogholiini*. Photos taken on Red Mountain, Mendocino Co., California, on 8 May 2018 by Jennifer Wheeler

Identification key to *Lomatium kogholiini* and similar species

These *Lomatium* species have similar leaf dissection. Bractlets are often wide and obovate, sometimes lobed or dissected, less often absent. Fruit walls are thick, and therefore oil ducts are obscure. Fruit wings are often curved down, making schizocarps elliptic in cross section, and usually about the same color as the fruit bodies. These species occur west of the Cascade Range and Sierra Nevada, mostly in California, though four occur in Oregon and southwest Washington.

1. Bractlets much dissected, sometimes 2-pinnate; Oregon (Willamette Valley) and southwest Washington ..... **Lomatium bradshawii**
1. Bractlets entire or sometimes few toothed or lobed, not pinnate, sometimes absent; southern Oregon and California.

2. Petals dark purple or dark red; nw. and central California.

3. Ultimate leaf segments ovate; mericarps length/width ratio 1.7–2.3 ..... **Lomatium ciliolatum** (in part)
3. Ultimate leaf segments linear; mericarps length/width ratio 1.1–2.

4. Peduncle densely scabrous; bractlets broadly scarious margined, rarely narrowly scarious margined; mericarps length/width ratio 1.4–2 ..... **Lomatium hooveri**
4. Peduncle glabrous to sparsely scaberulous; bractlets narrowly scarious margined; mericarps length/width ratio 1–1.6(–1.8) ..... **Lomatium marginatum** (in part)

2. Petals white, purplish-white, cream, or yellow; California and Oregon.

5. Petals white, purplish-white, or cream when fresh; anthers yellow, yellow-green, purple, or purple turning to cream; fruiting rays 1–4(–8) per umbel; mericarps 7–15 mm; s. Oregon and n. California.

6. Ultimate leaf segments (5–)10–84 mm; leaves green ..... **Lomatium marginatum** (in part)
6. Ultimate leaf segments 0.5–7(–18) mm, if segments up to rarely (–18) mm then leaves gray green (as in *L. peckianum*).

7. Ultimate leaf segments (1–)3–7(–18) mm; mericarps length/width ratio 2–3.8 (–4.4); fruit wings 1.2–2.8 mm wide; substrate volcanic ..... **Lomatium peckianum**
7. Ultimate leaf segments 0.5–3(–7); mericarps length/width ratio 1.7–3.6; fruit wings 0.5–1.5 mm wide; substrate strictly serpentine.

8. Ultimate leaf segment callus tips 0–0.1 mm; petals white; leaves green or blue-green; mericarps 4.8–10(–11.5) mm; fruiting pedicel 1–5(–6) mm; leaf surfaces glabrous; n. California ..... **Lomatium tracyi** (in part)
8. Ultimate leaf segment callus tips 0.1–0.2 mm, generally more pointed; petals purplish-white or white; leaves blue-green or gray-green, seldom green; mericarps 7–14 mm; fruiting pedicel (2–)3–9 mm; leaf surfaces glabrous, scabrous, or sparsely puberulent; s. OR and n. California ..... **Lomatium engelmannii**

5. Petals yellow when fresh; anthers yellow; fruiting rays 1–15 per umbel; mericarps 4.8–12(–13) mm; central California to s. Oregon.

9. Bractlets absent on most umbellets, if present on some then linear to lanceolate; ultimate leaf segments 0.5–10 mm; fruit wings 0.5–1.3 mm wide; California.

10. Rays 6–18 per umbel; leaf surfaces green or gray-green; oil tubes on the commissure 2–4; Red Hills of Tuolumne Co., California ..... **Lomatium congdonii**
10. Rays 4–7 per umbel; leaf surfaces green; oil tubes on the commissure 4–6; Red Mountain of Mendocino Co., California ..... **Lomatium kogholiini**

9. Bractlets present on most umbellets, or if absent on some umbellets then bractlets obovate to oblanceolate; ultimate leaf segments 0.5–60 mm; fruit wings 0.5–2.8 mm wide; California and Oregon.

11. Ultimate leaf segments elliptic to broadly ovate, 0.5–8 mm; peduncle 0.5–2 mm wide in fruit 1 cm below the umbel; California.

12. Leaves, peduncles, and/or rays glabrous or scabrous; bractlets obovate or oblanceolate, 1–2.5(–4) mm long; leaves pinnate to 1–2-pinnatifid; peduncle 0.5–1 (–1.2) mm wide in fruit; n. California ..... **Lomatium tracyi** (in part)
12. Leaves peduncles, and/or rays typically pubescent, sometimes glabrous or scabrous; bractlets usually obovate, 3–4 mm long; leaves usually more divided 1–2-pinnate to 2–3-pinnatifid; peduncle 0.5–2 mm wide in fruit; central and n. California.

13. Ultimate leaf segments 0.3–1 mm wide; substrate volcanic soil; range San Francisco Bay area (in Santa Clara and Stanislaus cos.) ..... **Lomatium observatorium**
13. Ultimate leaf segments 0.3–2.5 mm wide; substrate serpentine; range nw. California ..... **Lomatium ciliolatum**

11. Ultimate leaf segments linear, 2–60 mm; peduncle 0.5–4 mm wide in fruit 1 cm below the umbel; bractlets 1–10 mm; California and Oregon.

14. Leaves pinnate to 1–2-pinnatifid; peduncle 0.5–1(–1.2) mm wide in fruit; leaves, peduncles, and/or rays glabrous or scabrous; n. California ..... **Lomatium tracyi** (in part)
14. Leaves usually more divided 2–3-pinnate to 2–3-pinnatifid; peduncle 1–4 mm wide 1 cm below the umbel; leaves peduncles, and/or rays glabrous, scabrous, or pubescent; central and n. California.

15. Mature mericarps length/width ratio 1.7–3(–3.2); peduncle glabrous or distally scaberulous; southwest Oregon ..... **Lomatium cookii**
15. Mature mericarps length/width ratio 1–2.2; peduncle glabrous, scabrous, or pubescent; west-central California.

16. Bractlets usually >5 per fruiting umbellet, broadly obovate to narrowly oblanceolate, rarely lanceolate; mature fruiting pedicels 0.5–5(–6) mm, shorter than or equal to fruit length; peduncle glabrous, scabrous, or pubescent; elevation 50–600 m ..... **Lomatium caruifolium**
16. Bractlets usually <5 per fruiting umbellet, filiform to lanceolate, rarely narrowly oblanceolate; mature fruiting pedicels 3.5–13 mm shorter than or longer than fruit length; peduncle glabrous; elevation 250–1000 m ..... **Lomatium marginatum** (in part)

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Appendix 1. Additional specimens examined.

Lomatium caruifolium. **USA. California.** Butte Co.: 8 mi N of Oroville, 17 Apr1914, *A. A. Heller 11303* (OSC); 8 mi N of Oroville, 6 Mar 1915, *Heller 11769* (OSC). Mendocino Co.: Hog Hole Ridge, 552 m, 18 May 2018, *K. M. Mason 135A-135C* (OSC, SRP, UC); along Mountain House Road 9.6 km S of Hopland, 213 m, 20 May 1981, *Smith 6203* (CAS); wet serpentine outcrop at E edge of town of Boonville, Rte. 128, 400 ft, 21 May 1981, *Smith & Wheeler 6229A* (CAS). Sacramento Co.: Sacramento Valley; along Ca-104/Twin Cities Rd., 0.7 mi W of the Amador County Line (Carbondale 7.5' Q), 63 m, 7 Apr 2014, *Hemkamp & Barnes 22698* (OSC). San Francisco Co.: San Francisco, 25 Jun 1903, *E.R.S. S.10520* (ORE); San Francisco, Sierra and Missouri streets, 6 May 1956, *Howell 31353* (OSC); San Francisco, Hunters Point, 6 May 1957, *Howell 32217* (OSC); San Francisco, Bayview Hills, 18 Mar 1950, *Raven 1440* (OSC); San Francisco, McLaren Park, 30 Mar 1956, *Raven 8901* (OSC); San Francisco, NE of Mountain Lake, Presidio, 7 Apr 1957, *Raven 10595* (OSC); San Francisco, about the E summit of the San Miguel Hills, 13 Apr 1957, *Raven 10658* (OSC); San Francisco, Presidio Golf Links, 7 Apr 1956, *Rubtzoff 2181* (OSC). San Mateo Co.: E of SE end of San Andreas Lake; just W of Burlingame, near Millbrae, near junction of Trousdale Drive and Skyline Boulevard, between NW and SE versions of a new highway, 19 Apr 1968, *French 2858* (OSC [2 sheets]). Santa Barbara Co.: Santa Cruz Island, Central Valley, near valley Road 100 yards W of Reparo Viejo overlook., 1000 ft, 8 May 1990, *Junack sc-1670a* (OSC). Sonoma Co.: 4 mi N of Geyserville, 200 ft, 10 May 1942, *Constance & Rollins 2862* (ORE). Tuolumne Co.: S outskirts of Chinese Camp, 6 Apr 1968, *Constance et al. 3624* (OSC); along Hwy. #49, 2.1 mi. S of the jct of Hwy. #120 at Chinese Camp, 17 Apr 1973, *McNeal 1268* (OSC).

Lomatium congdonii. **USA. California.** Calavaras Co.: Highway 4 2.5 road mi N of Copperopolis; watershed Black Creek on gentle slope 0.3 mi E of the highway; Salt Spring Valley 7.5' USGS Quadrangle, 30 Apr 1998, *Taylor 16362* (UC); Highway 4 2.5 road mi N of Copperopolis, watershed Black creek on gentle slope 0.3 mi E of the highway, Salt Spring Valley 7.5' USGS Quadrangle, 6 Jun 1998, *Taylor 16487* (UC). Mariposa Co.: W Water Ditch [illegible] Mariposa, Jun 1896, *Congdon s.n.* (UC); Mariposa, 16 Apr 1893, *Congdon s.n.* (UC); West Water Ditch, 17 May 1903, *Congdon* (UC); West Water Ditch, Mariposa, 24 Jun 1894, *Congdon s.n.* (UC); Mariposa, 21 Apr 1897, *Congdon s.n.* (UC); Mariposa, 19 Apr 1996, *Congdon s.n.* (UC). Tuolumne Co.: 3 mi S of Chinese Camp on dirt road to La Grange, 1000 ft, 30 Mar 1956, *Constance et al. 3621* (UC); 3 mi S of Chinese Camp, 15 May 1937, *Hoover 2448* (UC); 3 mi S of Chinese Camp, 2 May 1939, *Hoover 4071* (UC); 3 mi S of Chinese Camp, rocky hills, 16 Jun 1967, *Hoove 10638* (UC); Jamestown, Red Hills, on Serpentine Loop Road, 338.5 m, 16 May 2018, *Mason 124* (UC); Red Hills, on the side of Red Hills Road, 351.4 m, 16 May 2018, *Mason 126* (SRP); Red Hills, rest stop off of Red Hills Rd closest to La Grange Road on a trail S side of rest stop, 368.6 m, 16 May 2018, *Mason 127* (OSC); Red Hills, NE-facing slope along dirt road into Sixbit Gulch., 1000 ft, 25 May 1984, *Taylor 8515* (UC); Peoria Basin, slopes at SE edge of basin ca. 1 mi E of Peoria Pass Rd, New Melones Dam 7.5' USGS Quadrangle, 900 ft, 15 Apr 1996, *Taylor 16332* (UC); Red Hills (ca. 3 air mi SW of Chinese Camp), 22 Apr 1998, *Taylor 16359* (UC).

***Lomatium engelmannii*. USA. California.** Siskiyou Co.: Scott Mts 5 mi above Callahan, 17 May 1954, *Barneby 11534* (CAS); 5.8 air mi SE of Callahan and 19 air mi SW of Weed, 15 May 2016, *McNeill s.n.* (CIC); margins of Carmen L., ca. 1.5 mi E of Scott Mt. road, 5700 ft, 28 May 1950, *Wiggins 12361* (OSC). **Trinity Co.**: Scott's Mountain Summit Campground off of Highway 3, 1650 m, 30 Jun 3028, *Mason 147* (SRP); about 1 mi S of Scott's Mountain Summit Campground off of Hwy 3 on the right hand side of the road heading north, 1584 m, 30 Jun 2018, *Mason 148* (OSC). **Oregon.** Curry/Josephine Co. line: E side of Kalmiopsis Wilderness Area, ridge N of Onion Camp, 7 Jun 1980, *Stansell s.n.* (OSC); Curry Co.: Ridge on divide between Chetco and Illinois Rivers, 4250 ft, 26 May 2004, *Duncan s.n.* (SOC); ridge, head of Slide Creek, 18 Jun 1930, *Leach 3034* (ORE). Josephine Co.: Along trail to Whetsone Butte from end of FR 4201, 4166 ft, 19 Jun 2013, *Duncan s.n.* (SOC); Chrome Ridge, 3990 ft, 17 May 1988, *Kagan 5178801* (OSC); E of Onion Mt., ca. 13 mi W of Grants Pass, 18 Apr 1989, *Paetzel s.n.* (OSC); Upper Pickett Cr. Region, ca. 12 mi W of Grants Pass, 25 May 1990, *Paetzel s.n.* (OSC); near a saddle about 2/5 mile ESE of Pearsoll Peak Summit, 4400 ft, 7 Jun 1992, *Rolle 551* (OSC); Chrome Ridge, 4000 ft, 29 May 1995, *Rolle 896* (OSC); Chrome Ridge, on Road 2402 0.5 mi north of jct with Road 2512, 21 Jun 1985, *Stansell & Planeto s.n.* (OSC).

***Lomatium tracyi*. USA. California.** Humboldt Co.: Horse Mtn., off Titlow Hill Rd. S of its junction with Hwy 2999 E of Arcata, 4900 ft, 23 Jun 1990, *Chambers 5517* (OSC); 1/4 mi from Horse Mtn Road, 1/2 mi below turnoff to summit, near end of unused gravel road, 1 May 1978, *Kelly 587* (UC); 1/4 mile from Horse Mtn Road, 1/2 mi below turnoff to summit, near end of unused gravel road, 1 May 1978, *Kelly 588, 589, 590,* and *591* (UC); intersection with road sign saying Grouse Mtn. L.O. 2 mi. Horse Mtn. 15 mi, 1 May 1978, *Kelly 592* (UC); Horse Mountain, 5000 ft, 20 Jun 1926, *Tracy 7610* (UC); Brannan Mountain, 10 Jul 1930, *Tracy 8869* (CAS, UC); Brannan Mountain, 3500 ft, 9 Jul 1933, *Tracy 12650* (UC); French Camp Ridge, 3500 ft, 23 Jun 1935, *Tracy 13971* (UC); Grouse Mountain, 5000 ft, 19 Jul 1949, *Tracy 18390* (UC). Lassen Co.: 4.5 mi E of Westwood on State Hwy 36, 16 Jun 1968, *Raven & Solbrig 13248* (UC). Shasta Co.: along road from Shingletown to Manton, 0.2 mi S of jct. with Rt. 44., roadside, 3200 ft, 16 Apr 1968, *Brehm 2907* (OSC); 2.6 mi NE of Ragan Meadow Public Camp where the Round Bottom Mine Road branches off, 2 Jul 1950, *Hoffman 3275* (UC). Trinity Co.: 1.5 mi above Peanut on State Hwy 36, 11 Jun 1948, *Ferris & Lorraine 11698* (CAS, UC); 3 mi NE of Douglas City, 26 Apr 1954, *Howell 29167* (CAS); top of low flat ridge that is partially encircled by a U-shaped bend in USFS road 35N23Y, ca. 100 m SE of its jct w/ USFS road 35N32Y, just W of Mule Creek, 2850 ft, 27 Jun 1984, *Jokerst 2078* (CAS); S of Peanut off Interstate 3 in the Trinity National Forest; Trinity stop #1, 870 m, 18 May 2018, *Mason 137* (SRP); on left hand side of heading E on Interstate 36 before Interstate 3 in Trinity National Forest, Trinity stop #2, 950 m, 19 May 2018, *Mason 138A* (SRP); on left hand side of heading E on Interstate 36 before Interstate 3 in Trinity National Forest, Trinity stop #2, 950 m, 19 May 2018, *Mason 138B* (UC); Hayfork Mountain, N of the town of Hayfork off Interstate 3 in the Shasta-Trinity National Forest, 1060 m, 19 May 2018, *Mason 146* (OSC); SW of South Dubakella Mtn W of road to Mud Springs, 5000 ft, 6 May 1978, *Nelson 4004* (UC); Dubakella Quad, Shasta-Trinity National Forest, Hill above road 29N55 at jct. with spur road, 5.6 mi S of jct with State Route 36., 5500 ft, 20 Jun 1980, *Nelson & Nelson 5683* (UC); Burns Ranch, 1500 ft, 28 Jun 1923, *Tracy 6393* (UC); Hay Fork Mountain, near summit on Weaverville Road., 3600 ft, 30 Jun 1923, *Tracy 6457* (UC); Mary Blaine Mt, 6400 ft, 3 Aug 1935, *Tracy 14462* (UC). Trinity-Shasta co. line: Jct. of Wildwood and Regan Meadow roads, 5000 ft, 2 Jul 1950, *Hoffman 3273* (UC). Trinity-Tehama co. line: Jct. of Wildwood and Regan Meadow roads, 5000 ft, 2 Jul 1950, *Hoffman 3273* (UC).

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Appendix 2. Samples used in the analyses, vouchers, GenBank numbers, and herbarium code following Thiers (continuously updated). All new samples are included here; data on other samples is available in Smith et al. 2018. DNA regions where amplification was not successful are indicated with NA. Voucher includes both the abbreviation used in Figure 1 and the collector and collection number as presented in Appendix 1. *Lomatium kogholiine* specimens listed as RMA to RME were leaves from additional Red Mountain plants, vouchered by *Mason 120*.

Taxon	Voucher	Herb.	State	County	Genbank Numbers						
					ITS	ETS	*rpl32-trnL*	*rps16* intron	*trnD-trnT*	*ndhF-rpl32*	*psba-trnH*
L. caruifolium	HH1 = Mason 135A	UC	CA		MK178380	MK178330	MK178405	MK178455	MK178479	MK178430	MK178355
	HH2 = Mason 135B	OSC	CA		MK178381	MK178331	MK178406	MK178456	MK178480	MK178431	MK178356
	HH3 = Mason 135C	SRP	CA		MK178382	MK178332	MK178407	MK178457	MK178481	MK178432	MK178357
	LC = Constance 3622	OSC	CA	Amador	NA	MK178334	NA	NA	NA	NA	MK178359
	LA = Ahart 12562	OSC	CA	Butte	MK178383	MK178333	MK178408	MK178458	MK178482	MK178433	MK178358
L. congdonii	RH1 = Mason 124	UC	CA		MK178384	MK178335	MK178409	MK178459	MK178483	MK178434	MK178360
	RH2 = Mason 126	SRP	CA		MK178385	MK178336	MK178410	MK178460	MK178484	MK178435	MK178361
	RH3 = Mason 127	OSC	CA		MK178386	MK178337	MK178411	MK178461	MK178485	MK178436	MK178362
L. engelmannii	K. Mason 147	SRP	CA	Trinity	MK178387	NA	MK178412	MK178462	MK178486	MK178437	MK178363
	K. Mason 148	OSC	CA	Trinity	MK178388	MK178338	MK178413	MK178463	MK178487	MK178438	MK178364
	MP sn = Paetzel s.n.	OSC	OR	Josephine	MK178389	MK178339	MK178414	MK178464	MK178488	MK178439	NA
	R. P. McNeill sn	CIC	CA	Siskiyou	MK178390	MK178340	MK178415	MK178465	MK178489	MK178440	NA
	VS sn = Stansell s.n.	OSC	OR	Curry / Josephine	MK178391	MK178341	MK178416	MK178466	NA	MK178441	MK178365
L. marginatum	DF = French 2864	OSC	CA	Lake	MK17	NA	NA	NA	NA	NA	MK17

					8392						8366
	LC = Constance 3289	OSC	CA	Shasta	MK17 8393	MK17 8342	MK17 8417	NA	NA	MK17 8442	MK17 8367
	RH 9011 = Halse 9011	OSC	CA	Glenn	MK17 8394	MK17 8343	MK17 8418	MK17 8467	NA	MK17 8443	MK17 8368
L. kogholiine	RM1 = Mason 120	OSC	CA	Mendocino	MK17 8374	MK17 8324	MK17 8399	MK17 8449	MK17 8473	MK17 8424	MK17 8349
	RMA, Mason		CA	Mendocino	MK17 8375	MK17 8325	MK17 8400	MK17 8450	MK17 8474	MK17 8425	MK17 8350
	RMB, Mason		CA	Mendocino	MK17 8376	MK17 8326	MK17 8401	MK17 8451	MK17 8475	MK17 8426	MK17 8351
	RMC, Mason		CA	Mendocino	MK17 8377	MK17 8327	MK17 8402	MK17 8452	MK17 8476	MK17 8427	MK17 8352
	RMD, Mason		CA	Mendocino	MK17 8378	MK17 8328	MK17 8403	MK17 8453	MK17 8477	MK17 8428	MK17 8353
	RME = Mason		CA	Mendocino	MK17 8379	MK17 8329	MK17 8404	MK17 8454	MK17 8478	MK17 8429	MK17 8354
L. tracyi	KLC = Chambers 5517	OSC	CA	Humboldt	MK17 8396	MK17 8345	MK17 8420	MK17 8469	MK17 8490	MK17 8445	MK17 8370
	BGB 2907 = Brehm 2907	OSC	CA	Shasta	MK17 8395	MK17 8344	MK17 8419	MK17 8468	NA	MK17 8444	MK17 8369
	T1 = Mason 137	SRP	CA		MK17 8397	MK17 8346	MK17 8421	MK17 8470	MK17 8491	MK17 8446	MK17 8371
	T2 = Mason 138A	SRP	CA		MK17 8398	MK17 8347	MK17 8422	MK17 8471	MK17 8492	MK17 8447	MK17 8372
	T3 = Mason 146	OSC	CA		NA	MK17 8348	MK17 8423	MK17 8472	MK17 8493	MK17 8448	MK17 8373

Appendix 3. Geolithology and geocomposition of ultramafic bedrock in the areas where four *Lomatium* grow in northern California, from USGS (2018). The age of the ultramafic rock can have an influence on the proportion of serpentine plant endemics, perhaps due to time periods for weathering to occur and for adaptation to ultramafic soils (Brooks 1985). KM = Klamath Mountains. CR = Coast Range and western Klamath Mountains.

	Lomatium kogholiini	***Lomatium tracyi***	***Lomatium engelmannii***	***Lomatium congdonii***
Geologic unit	3 (southern region)	2 (and 3?)	1	2
Major Rock	Serpentinite	Serpentinite amd Peridotite	Peridotite	Serpentinite and Peridotite
Minor Rock	Peridotite	Pyroxenite	Serpentinite and Pyroxenite	Pyroxenite
Ultramafic Zone (Range and Age)	Coast Ranges and Western Klamath Mountains	Western Sierra Nevada and KM and possibly CR	Trinity Ophiolite	Western Sierra Nevada and Klamath Mountains
Age	Middle to late Jurassic (youngest)	KM: Late Proterozoic (?) to early Jurassic CR: Middle to late Jurassic	Ordovician (oldest)	Later Proterozoic (?) to early Jurassic

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ADENOPHYLLUM POROPHYLLUM (ASTERACEAE) REPORTED FOR ARIZONA AND THE USA, WITH A KEY TO SPECIES

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ABSTRACT

Adenophyllum porophyllum is reported for the Arizona and USA flora. Its presence north of the Mexican border was overlooked for Flora of North America but only a single collection was made before 2006 (in 1984); others have been made from 2011 to 2018. Photographs, a species key for the genus in Arizona, and brief species descriptions are provided.

RESUMEN

Se reporta *Adenophyllum porophyllum* para la flora de Arizona y los Estados Unidos. Su presencia al norte de la frontera con México fue pasada por alto en Flora of North America pero solo una colecta fue hecha antes de 2006 (en 1984); otras se han realizado desde 2011 hasta 2018. Se proporcionan fotografías, una clave para especies del género en Arizona, y descripciones breves de especies.

While documenting the vascular flora of the Salero Ranch in central Santa Cruz Co., Arizona (Carnahan, in prep.), I made several collections of a rayless, annual composite that I provisionally identified as *Adenophyllum porophyllum* (Cav.) Hemsl. John Strother kindly confirmed my determination from photographs (Strother, pers. comm., 7 May 2018). The presence of *A. porophyllum* in the USA was overlooked for the Flora of North America (Strother 2006). A search of the SEINet Portal Network (SEINet 2019) indicates that a 1984 voucher (*Luetcke s.n.*, ARIZ) from the Mule Mountains in Cochise County is apparently the earliest collection from the state, followed by others beginning in 2011 (citations below).

With the addition of *Adenophyllum porophyllum,* five *Adenophyllum* taxa are known to occur in the USA.

Adenophyllum cancellatum (Cass.) Villareal
Adenophyllum cooperi (A. Gray) Strother
Adenophyllum porophylloides (A. Gray) Strother
Adenophyllum porophyllum (Cav.) Hemsl.
Adenophyllum wrightii A. Gray

Adenophyllum cancellatum occurs in the Central Plateau in Mexico and is known in trans-Pecos Texas from two collections (*Manning 5077,* SRSC, *Taylor 390*, SRSC; Powell & Worthington 2018). The other four taxa are documented for Arizona. A sixth species, *A. anomalum* (Canby & Rose) Strother, occurs in northwestern Mexico and has been collected within 20 miles of the Arizona border (e.g., W base of Sierra de Los Pinitos, E of Cibuta, *Van Devender 2005-539*, ARIZ).

Lack of a complete key to *Adenophyllum* in Arizona may have led to misidentifications. A key to *A. cooperi, A. porophylloides,* and *A. wrightii* is provided in Flora of North America (Strother 2006) and in Kearney and Peebles (1960) within the genus *Dyssodia*. McVaugh (1984) and Turner (1996) treated the Mexican species of *Dyssodia,* including those later transferred to *Adenophyllum* (Strother 1986). Turner (2013) included a key to *Adenophyllum* species near Yécora, Sonora (*A. cancellatum, A. porophyllum,* and *A. yecoranum* B.L. Turner). Spellenberg and Anderson (2010)

reported *A. porophyllum* for Chihuahua, Mexico, and noted its lack of ray flowers. The Malezas de Mexico website (Vibrans 2006) points out the difference between *A. porophyllum* and *A. cancellatum*.

The following key and descriptions pull together information from specimens and previous publications.

ADENOPHYLLUM Pers.

The genus *Adenophyllum*, formerly treated in *Dyssodia* (Strother 1969, 1986; see also Turner 1996), includes 11 species of annuals, perennials, and subshrubs. Leaves opposite below and mainly alternate above, entire or lobed, the lobes entire or toothed. Leaves and involucres with yellowish oil glands producing a skunk-like odor. Involucres usually with calyculi (outer bracts), these with entire or pectinate margins; phyllaries (inner bracts) fused at least at the base and generally no more than 1/3–2/3 their length. Heads discoid or radiate; ray florets (when present) pistillate, fertile, corollas yellow to red-orange; disk florets bisexual, fertile, corollas yellow to red-orange. Pappus mostly of scales divided into bristles; achenes compressed, glabrous to pubescent. Within the USA, *Adenophyllum* occurs only in Arizona, California, Nevada, New Mexico, Texas, and Utah.

Key to *Adenophyllum* species in the USA and northern Sonora

1. Calyculi with pectinate margins; phyllaries often with "horned" gland near apex; ray flowers present or absent.
   2. Ray flowers present and showy; trans-Pecos Texas and Mexico; not known in Arizona ..... **Adenophyllum cancellatum**
   2. Ray flowers absent; southeastern Arizona ..... **Adenophyllum porophyllum**

1. Calyculi with entire margins; phyllaries without "horned" gland near apex; ray flowers present (though sometimes small).
   3. Subshrubs, woody at base; mostly deserts in central and western Arizona.
      4. Herbage gray-green and minutely hispidulous; leaves mostly oval or ovate (rarely with 3 or more lobes); ligules of ray flowers 8–12 mm; Mojave Desert in northwestern Arizona ..... **Adenophyllum cooperi**
      4. Herbage green and essentially glabrous; leaves mostly with 3–5 lobes; ligules of ray flowers less than 7 mm; Sonoran Desert in central and western Arizona ...**Adenophyllum porophylloides**
   3. Annuals to short-lived perennials, not usually woody at base; mostly above the desert.
      5. Involucres 7–8 mm; calyculi without glands; ligules of ray flowers 2–6 mm; pappus of 2 layers: outer of erose scales to 1 mm, inner of scales dissected into bristles, 8 mm; rare in mountains of east-central Arizona ..... **Adenophyllum wrightii**
      5. Involucres 3.5–4.5 mm; calyculi usually with glands; ligules of ray flowers 8–10 mm; pappus of scales dissected into bristles; not known north of Sonora ..... **Adenophyllum anomalum**

1. Adenophyllum anomalum (Canby & Rose) Strother
Dyssodia anomala (Canby & Rose) B.L. Rob.
Hierba del zorrillo, rosita

Annuals to short-lived perennials. Leaves 3–5 cm long, pinnatifid with 3–9 filiform segments. Calyculus of 1–4 narrow bracts with entire margins, or calyculus absent; phyllaries in 2 series, 4 mm long; calyculi and phyllaries with inset oil glands. Heads radiate; ligules of ray flowers 8–10 mm; disk and ray corollas yellow. Achenes 2–2.5 mm long; pappus of scales divided into bristles, 3 mm long. Flowering spring and fall. Oak woodland just south of the Arizona–Sonora border, southward in thornscrub and tropical deciduous forest to Durango; also at the desert edge near Guaymas, Sonora (Felger et al. 2017). It should be looked for along the Arizona–Sonora border.

2. Adenophyllum cancellatum (Cass.) Villareal
Adenophyllum porophyllum var. *cancellatum* (Cass.) Strother
Dyssodia porophyllum. var. *cancellata* (Cass.) Strother
Cimpasúchil

Robust annuals 0.4–0.7 m tall, branching above the middle. Leaves alternate, pinnatifid with 3–9 lobes, the lobes toothed. Calyculus of 12–20+ narrow bracts with pectinate margins; phyllaries 10–13 mm; calyculi and phyllaries with prominent oil glands. Heads radiate; ligules of ray flowers to 9 mm; disk and ray corollas yellow to yellow-orange. Achenes 4–5 mm; pappus of scales dissected into bristles, 8–9 mm. Flowering August–November. Grassland, thornscrub, and tropical deciduous forest in the Central Plateau of Mexico, including Chihuahua and southern Sonora, plus 2 roadside collections (waifs?) from trans-Pecos Texas (Powell & Worthington 2018).

In his treatment of the genus *Dyssodia* (1969, 1986), Strother considered *Adenophyllum cancellatum* a variety of *A. porophyllum,* differing from it mainly by the presence of ray flowers. McVaugh (1984) also treated the two taxa at the varietal level but commented that "The two sometimes occur together in nature and are occasionally confused by collectors. …. They differ rather strikingly, however, not only in the obvious characters used in the key, but in other more subtle features of flowers and involucre" (1984: 309). I follow the lead of Villareal (2001), who noted the lack of intergrading specimens in mixed populations and treated both at species rank, as did Turner (2013).

3. Adenophyllum cooperi (A. Gray) Strother
Dyssodia cooperi A. Gray
Cooper's dogweed

Perennial herbs to subshrubs, woody at base, to 0.6 m tall. Herbage gray-green and minutely hispidulous. Leaves usually oval or ovate (sometimes with 3 or more shallow lobes), with spinose-toothed margins. Calyculus of 12–20+ narrow bracts with entire margins; phyllaries 10–17 mm long; calyculi and phyllaries with inset oil glands. Heads radiate; ligules of ray flowers to 12 mm (occasionally ray flowers absent); disk and ray corollas yellow to red-orange. Achenes 5–6 mm; pappus of scales dissected into bristles, 8–12 mm. Flowering spring and fall. Mojave Desert in northwestern Arizona, also California, Nevada, and Utah.

4. Adenophyllum porophylloides (A. Gray) Strother
Dyssodia porophylloides A. Gray
San Felipe dogweed

Perennial herbs to subshrubs, woody at base, to 0.6 m tall. Leaves pinnatifid with 3–5 narrow lobes. Calyculus of 12–20+ narrow bracts with entire margins ; phyllaries 9–16 mm; calyculi and phyllaries with inset oil glands. Heads radiate; ligules of ray flowers to about 6 mm; disk and ray corollas orange to red-orange. Achenes 4–5 mm long; pappus of scales dissected into bristles, 8–10 mm. Flowering spring and fall. Sonoran Desert in central and western Arizona, also Nevada, California, and Mexico in Baja California, Baja California Sur, and northwestern Sonora.

5. Adenophyllum porophyllum (Cav.) Hemsl.
Dyssodia porophyllum (Cav.) Cav.
Pore-leaf dogweed, *árnica del monte*

Robust annuals 0.4–0.8 m tall, branching above the middle. Leaves alternate, pinnatifid with 3–9 lobes, the lobes toothed. Calyculus of 12–20+ narrow bracts with pectinate margins; phyllaries 10–13 mm; calyculi and phyllaries with prominent oil glands. Heads discoid; disk corollas yellow to red-orange. Achenes 4–5 mm; pappus of scales dissected into bristles, 8–9 mm. Flowering August–October. Grassland and oak savanna in southeastern Arizona, also grassland, thornscrub, and tropical deciduous forest in Sonora and Chihuahua, Mexico, southward to Guatemala. It should be looked for in southern New Mexico.

Figure 1. *Adenophyllum porophyllum.* (A) Salero Ranch, Santa Cruz Co., Arizona. 13 Sep 2013. (B) Santa Rita Mountains, Santa Cruz Co., 22 Sep 2018. (C) Salero Ranch, Santa Cruz Co., 20 Sep 2015. (D) Salero Ranch, Santa Cruz Co., 29 Sep 2011. Photographs by Susan D. Carnahan.

Specimens reviewed. **Arizona**. Cochise Co.: Mule Mountains, Dixie Canyon, 25 Sep 1984, *Luetcke s.n.* (ARIZ); Fort Huachuca, between lower Garden and Huachuca Canyons, 26 Sep 2011, *Setaro s.n.* (ASU); Huachuca Mountains, between Brown and Ramsey canyons, 27 Sep 2013, *Setaro s.n.* (ASU). Santa Cruz Co.: Salero Ranch, Grosvenor Rd, 8 mi SE of Tubac, 13 Sep 2013, *Carnahan SC 160* (ARIZ); County Rd 58, SE of Patagonia, 21 Sep 2014, *Wolkis & Setaro s.n.* (ASU); Elgin, Southmoreland Pl., 11 Oct 2014, *Robinett 336* (ARIZ); Research Ranch, S of Cimarron Rd in Coronado Natl Forest, 20 Oct 2014,

Kennedy 338 (ARIZ); Salero Ranch, SSW of Salero HQ, 20 Sep 2015, *Carnahan 1508* (ARIZ); Santa Rita Mts, Forest Service Rd 143 S of Montosa and Cottonwood canyons, Coronado Natl Forest, 31 Aug 2018, *Carnahan 3331* (ARIZ).

6. Adenophyllum wrightii A. Gray
Dyssodia neomexicana (A. Gray) B.L. Rob.
Wright's dogweed

Annuals 20 to 40 cm tall. Leaves pinnatifid with 7–13 filiform lobes. Calyculus of 6–8 narrow, linear bracts with entire margins, lacking oil glands; phyllaries 5–9 mm, with inset oil glands. Heads radiate; ligules of ray flowers 2–6 mm; disk and ray corollas yellow. Achenes 3–5 mm; pappus of two series: outer series of erose scales to 1 mm, inner series of scales dissected into bristles, to 8 mm long. Flowering (July) August–October. Rare in mountains of east-central Arizona, also New Mexico and northern Chihuahua, Mexico.

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DOS ESPECIES NUEVAS DE *NOLINA* (ASPARAGACEAE) DEL CENTRO DE MÉXICO

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RESUMEN

Se describen e ilustran dos nuevas especies, **Nolina orbicularis** L. Hern., **sp. nov.**, del centro de la Faja Volcánica Transmexicana y montañas de origen ígneo al sur de la Mesa Central de México, así como **Nolina robusta** L. Hern., **sp. nov.**, del sur de la Sierra Madre Oriental. Dado que materiales de herbario correspondientes se han determinado como *N. parviflora* (Kunth) Hemsl. o *N. hibernica* Hochstätter & D. Donati se presentan características diagnósticas para diferenciar los cuatro taxones.

ABSTRACT

Two new species, **Nolina orbicularis** L. Hern., **sp. nov.**, from the Transmexican Volcanic Belt and mountains of igneous origin to the south side of the Mexican Mesa del Centro, and **Nolina robusta** L. Hern., **sp. nov.**, from the southern portion of the Sierra Madre Oriental, are described and illustrated. Herbarium vouchers have been commonly misidentified as *N. parviflora* (Kunth) Hemsl. or *N. hibernica* Hochstätter & D. Donati. A key and a table with diagnostic characters to distinguish the four species are included.

Durante la revisión de materiales de herbario y el trabajo de campo para Flora del Bajío y de regiones adyacentes, se encontraron especímenes del género *Nolina* que generalmente se han identificado como *N. parviflora* (Kunth) Hemsl. o *N. hibernica* Hochstätter & D. Donati. Al revisar ejemplares en campo, en herbarios, así como la bibliografía asociada a estas entidades (Hemsley 1884; García-Mendoza 2010; Hochstätter & Donati 2010; Ruíz-Sánchez & Specht. 2014), se propone que representan dos especies no descritas para el género.

NOLINA ORBICULARIS L. Hern., **sp. nov. TIPO: MÉXICO**. **San Luis Potosí**. Mpio. Villa de Zaragoza: 24 km al SE de Villa de Zaragoza, ca. 3 km al NE de La Salitrera, 21° 57' 15" N, 100° 33' 56" O, elev. 2270 m, 31 ago 2018, *L. Hernández 7900* (holotipo: QMEX; isotipos MEXU, XAL, IEB, UASLP). Figuras 1 y 2.

Similar to *N. parviflora* (Kunth) Hemsl. in the arborescent habit, straight leaf apices, and inflorescence length but different from it by its shorter (67–92 cm long) and narrow linear leaves (1.4–1.6 cm wide) with a slight constriction above the base, entire apices; inflorescence branches divaricate, staminate flower pedicels 4–5 mm long articulated at 1/3 from the base, pistillate flowers 2–4 per node, with ovules subtended by a globose to callous-like protuberance, and fruits orbicular in general shape.

Plantas dioicas, arborescentes de (1)3 a 5 m de alto; **troncos** de una o dos veces ramificados en la parte superior, con rosetas foliares terminales de ca. 1 m de diámetro y follaje marcescente bajo estas y no a lo largo de toda la rama o de los tallos, hojas viejas deprimidas a descendentes, corteza largamente fisurada con textura corchosa gruesa en la base de la planta; **hojas** lineares, de 67 a 92 cm de largo por 1.4 a 1.6 cm de ancho, con una ligera constricción arriba de la base, márgenes denticulados con dientes de ca. 0.1 mm de largo, 1 a 2 dientecillos por mm, quebradizos, con 1 a 3 cúspides por diente, de color rojizo con la edad, base de la hoja triangular, de 4 a 7 cm de largo, 4 a 6 cm de ancho en la parte inferior y 2 a 2.5 cm de ancho en la superior, ápices curvados, a veces rompiéndose pero sin formar fibras; **inflorescencia** una panícula de 1 a 2 m de largo, brácteas del

escapo lineares, de ca. 43 cm de largo por ca. 3 cm de ancho en la base, de color café amarillento pajizo, ramas de la inflorescencia divaricadas a difusas, de hasta 25 cm de largo, con ramillas secundarias hasta de 9 cm de largo en la base y hasta 1 cm en el ápice, la ramilla terminal central de 5 a 10 cm de largo, todas con nudos de flores laxamente distribuidos, brácteas subyacentes a ramas y ramillas lineares a lanceoladas, hasta de 14 cm de largo por 3 cm de ancho en la base, con márgenes dentados a fimbriados; **flores estamina**das de 4 a 5 mm de diámetro, (2)3 a 4(8) por nudo, sobre pedicelos de 4 a 5 mm de largo, articulados a 1/3 de la base y llevando en la base bractéolas lineares, las externas de hasta 5 mm de largo y las internas de ca. 2 mm de largo, tépalos lanceolados, de ca. 3 mm de largo de 1.5 a 2 mm de ancho, blancos a color crema, estambres de ca. 2 mm de largo, anteras sagitadas, de ca. 1 mm de largo, insertas en el centro, ovario poco desarrollado, hasta de 2 mm de diámetro, funcionando como nectario; **flores pistiladas** de 2 a 4 por nudo, sobre pedicelos de 2 a 4 mm de largo, articulados debajo de la mitad o hacia la base, cada pedicelo con una bracteola triangular subyacente y todas rodeadas por una bractéola largamente triangular, de 3 a 4 mm de largo, membranácea, blanca a color crema con los márgenes fimbriados, tépalos de 2.5 a 3 mm de largo, blancos a color crema con la parte central ligeramente obscurecida, ovario trilocular, óvulos 2 por lóculo, a una distancia de 0.75 a 1 mm de la base, sobre un engrosamiento a manera de repisa o a veces globoso, de ca. 0.5 m de ancho, estaminodios 6; **frutos** 2 a 4 por nudo, sobre pedicelos de 6 a 8 mm de largo, articulados a los 2 a 4 mm de la base, trilobados, casi orbiculares, de ca 0.8-0.9 cm de largo por ca. 1 cm de ancho, lóbulos con un margen ligeramente engrosado, hendidura apical de hasta 3 mm de profundidad, tépalos persistentes con la parte media engrosada formando una quilla; **semillas** ovadas a anchamente fusiformes, de 4 a 5 mm de largo por 3 a 4 mm de ancho, testa casi lisa de color marrón claro o amarillento.

Material adicional examinado. MÉXICO. **San Luis Potosí**. Mpio. Mexquitic de Carmona: carretera a Ahualulco ca. a 500 m de El (San) Salvador, 22° 20' 44" N, 100° 04' 16" W, elev. 2200 m, 23 jul 1988 (fr), *Puente 263* (IBUG, UASLP). Mpio. Río Verde: El Aguijón, 28 km al SSW de Río Verde, 21º 40' 23" N, 100º 03' 15" W, elev. 1780 m, 8 jun 1956 (fl.♀ y fr.), *Rzedowski 7688* (IEB, TEX); carretera Río Verde-San Ciro y luego 21 km al SW hacia El Realito, 21º 41.37' N, 100º 02.13" W, elev. 1475 m, 6 jun. 1999 (fl.♀ y fr. jóvenes), *Hernández 4352* (QMEX). Mpio. Villa de Zaragoza: 1 km al SE del poblado El Xoconoxtle, cerro Las Aguilas, elev. 2110 m, 31 jul. 2002 (fl.♂), *García 3778* (UASLP); 16 km al SE de Villa de Zaragoza, ca. 0.5 km al E de El Ranchito de Juárez, 21° 57' 33.31" N, 100° 37'3. 55" O, elev. 2070 m, 31 ago 2018 (fr.), *Hernández 7893* (QMEX). **Guanajuato**. Mpio. San Luis de la Paz: 13 km E de San Luis de la Paz, 2 km al E de San Miguel de las Casas, 21º 18.26' N, 100º 10.37' W, elev. 2490, 20 ago 1997 (fl.♂), *Hernández 4279* (QMEX). Mpio. Xichú: carretera Xichú - San Luis de la Paz, 21º 18' 45" N, 100° 14' 13.2" W, elev. 2233 m, 22 jun 2012 (fr.), *Magallán 496* (QMEX); 13.5 km al W de Xichú por la carretera a San Luis de la Paz, 21° 18' N, 100° 04' W, elev. 1800 m, 31 may 1996 (fr.), *Zamudio 9804* (IEB, TEX). Mpio. Victoria: alrededores de Milpillas del Pito, 21º 20' 07.5" N, 100º 14' 05.25" W, elev. 2250 m, (fr.), *Rzedowski 50961* (IEB, QMEX); 2.7 km al ENE en línea recta de Puerto del Aire, 21º 18' 51" N, 100º 10' 32" W., elev. 2370 m, 16 jul 2011 (estéril) *Carrillo y Carranza 6370* (IEB, QMEX); Charco Azul, ca. 15 km de Xichú a San Luis de la Paz o 6 km en línea recta, 21º 18' 50" N, 100ª 06' 31" W, elev. 2270 m, 18 jun 2018 (fr.), *Hernández 7798* (QMEX); 1 km al N del Puerto del Peltre, hacia Xichú, 21º 18.76' N, 100º 14.22' W, elev. 2276 m, 24 mar 2008 (fl.♂.), *Hernández 6059* (QMEX); Río Colorado, 14 jun 1990 (fr.), *Ventura y López 8103* (IEB, QMEX). Mpio. Jerécuaro: Puerto del Yesero, 20° 08' 30" N, 100° 30' 06" W, elev. 2700 m, 24 oct 1986, *Díaz-Barriga 3288* (IEB). **Querétaro**. Mpio. El Marqués: 3 km al S de la Laborcilla, 14 sept. 1990, *S. Zamudio y E. Pérez* 8102 (IEB).

La especie se distribuye en la parte central de la Faja Volcánica Transmexicana y serranías de origen ígneo al sur de la Mesa Central de México, en los estados de Guanajuato, San Luis Potosí y Querétaro. Se encuentra en bosques de encino, de pino encino con *Arbutus* y en matorrales rosetófilos a veces en transición con matorrales espinosos, sobre pendientes pronunciadas en altitudes que van desde los 1300 a los 2700 msnm. Presenta flores de marzo a agosto y frutos de mayo a octubre. En las poblaciones naturales del área de estudio presenta pocos individuos, por lo que se

considera como una especie rara que deberá ser protegida para su conservación. En la región se le conoce con el nombre común de "soyate."

Figura 1. Holotipo de *Nolina orbicularis*. Planta con frutos, presentando rama y brácteas de la inflorescencia, así como hojas maduras.

Figura 2. Ejemplar de *Nolina orbicularis* con flores estaminadas.

NOLINA ROBUSTA L. Hern., **sp. nov. TIPO: MÉXICO. Querétaro**. Mpio. Cadereyta: 5 km al NW de El Doctor, 20º 50' 59" N, 99º 36' 14" W, elev. 2800 m, 11 oct 1987, *J. Rzedowski 45033* (holotipo QMEX; isotipo IEB). Figura 3.

Similar to *Nolina hibernica* Hochstätter & D. Donati in the arborescent habit and marcescent branches but different from it by its larger plant size, up to 7 m tall, leaves with erect and shredded fibrous apices, inflorescence up to 2.5 m long, erect to adpressed branches, staminate flowers 2–2.5 mm diameter on pedicels 3–4 mm long articulated at the middle, ovules in pistillate flowers subtended by a protuberance, and fruit lobes with margin absent or very thin.

Plantas dioicas, arborescentes de 2.5 a 7 m de alto, pueden llegar a ser masivas, de forma general largamente obcónica, con 1 a 2(4) ramas con rosetas foliares terminales de hasta 1 m de diámetro, follaje marcescente comúnmente a lo largo de toda la rama o del tallo, hojas viejas deprimidas; **hojas** lineares, de 70 a 130 cm de largo por 2 a 3 cm de ancho, con las bases deltoideas de 5 a 13 cm de largo por 9 a 11.5 cm de ancho en la parte inferior y 2.5 a 3.5 cm de ancho en la superior, márgenes de hoja microdenticulados con los dientecillos translúcidos a amarillentos y de color marrón con la edad, simples o a veces 3-cuspidados, orientados indistintamente hacia el ápice o a la base de la hoja, ápice desintegrándose y a veces quedando en forma de fibras; **inflorescencia** paniculada, de hasta 2.5 m de alto con ramas de hasta 32 cm de largo, erectas a casi adpresas, las más grandes con hasta 6 ramillas en la base (3 de ca. 15 cm y 3 de ca. 6 cm de largo), llevando en la base brácteas largamente triangulares a lineares de hasta 30 cm de largo en las ramas mayores con ápices curveados, ramillas erectas a sinuosas, delgadas, las basales de hasta 12 cm de largo en las ramas mayores, de hasta 1 cm en las apicales, **flores** con 2 bractéolas fimbriadas subyacentes, la mayor de 2.5 a 3.5 mm de largo y la menor de 1.5 a 2 mm de largo; **flores estaminadas** 2 por nudo sobre pedicelos de 3 a 4 mm de largo, articulados cerca de la mitad, ocasionalmente se encuentra una bractéola adicional en la parte articulada, tépalos lanceolados, de 3 a 3.5 mm de largo por 1.5 a 2 mm de ancho, de color crema, con tricomas apicales, filamentos de ca. 2.5 mm de largo, anteras amarillas, de 1.5 a 2 mm de largo, sagitadas con inserción media, ovario no desarrollado, de 1 a 1.2 mm de diámetro, funcionando como nectario; **flores pistiladas** 2 a 4 por nudo, lanceolados, de 2 a 2.5 mm de largo por ca.1.5 mm de ancho, de color blanco a crema, ovario trilocular, óvulos 2 por lóculo, ubicados cerca o abajo de la mitad del ovario, sobre un engrosamiento a manera de callo, estaminodios 6; **frutos** sobre pedicelos de 6 a 8 mm de largo, articulados a 1/3 de la base, globulares, deprimidos, de 0.8 a 0.9 cm de largo por 1 a 1.1 cm de ancho, con 3 lóbulos, hendidura apical de hasta 3 mm de profundidad, tépalos persistentes con un callo en la base; semilla 1 por lóculo, fusiforme, de ca. 3 mm de largo por ca. 2 mm de ancho, testa de color marrón rojizo.

Material adicional examinado. MÉXICO. **San Luis Potosí.** Mpio. Xilitla: Llano de La Garza, 3.5 km al N-NO de la comunidad de La Trinidad, 11 jun 2015, *Castillo 1403* (QMEX, SLPM). **Querétaro**. Mpio. Arroyo Seco: 8 km al W de Puerto Ayutla, 21º 20' 31.7" N, 99º 36' 06.7" W, elev. 1328 m, 23 jun 2002 (fl.♀.), *Hernández 4883* (QMEX); ± 10 km de Puerto de Ayutla, camino a Santa María de Cocos, 27 ago 1989 (fl.♂.), *Carranza 1900* (IEB). Mpio. Jalpan: 8 a 10 km al norte de La Parada, rancho La Soledad, elev. 1000 m, 6 jun 1991 (fr.), *Servín 1083* (IEB, QMEX); ladera NW del Cerro Grande ± 8 km as SE de San Juan de los Durán, 7 abr. 2011, *Zamudio et al. 15085* (IEB); ladera O del cerro Grande, 21° 26' 00.4" N, 99° 08' 24.2" W, elev. 2400 m, 28 mar 2012, *Aguilar et al. 802* (IEB, MEXU). Mpio. Landa de Matamoros: 1.5 km al poniente de Puerto Hondo, 21° 12' 58" N, 99° 06' 33" W, 1850 m, 16 may 1990 (fr.), *Rubio 1652* (IEB, MEXU, QMEX, XAL), (fl.♂.), *Rubio 1653* (IEB, MEXU, QMEX, XAL); parte alta del cerro Grande ± 9 km al SE de San Juan de los Durán, 11 mar. 2011, *Zamudio et al. 15069* (IEB),*15070* (IEB). Mpio. Cadereyta: Los Juárez, 99° 39' N, 20° 52' W, elev. 2750 m, 11 may 1978, *Zamudio 2822* (IEB); parador El Tepozán, 20º 54.402" N, 99º 38.934" W, elev. 2360 m, 8 mar 1996, *Zamudio 9763* (IEB, QMEX), 18 mar 1998, *Zamudio 10652a* (IEB, QMEX), (fr.) *10653* (IEB, QMEX); ibid., 19 mar 1998 (fl.♂), *Hernández 4287* (IEB, QMEX), (fr.) *4287a* (IEB, QMEX); Sierra El Doctor, cerca de las antenas, 1 km al N de La Lagunita (a 5 km de Sombrerete), 20° 50' 23.3" N, 99° 35' 15.4" W, elev. 3000 m, 25 abr 1997, *Hernández 4176* (QMEX), ibid. elev. 3020, 12 may 1997, *Hernández 4184*

(QMEX); 2 km al N de La Lagunita, 20° 50' 24.66" N, 99° 35' 15.4" W, elev. 3000 m, 10 may 2008, *Hernández 6045* (IEB, QMEX), *6046* (IEB, QMEX); Sierra El Doctor, cerro La Cabeza, 5 km al SW de Vizarrón, 20° 49' 54" N, 99° 43' 12" W, elev. 2580 m, 30 abr 1978 (fr.), *Zamudio 2771* (IBUG, IEB, MEXU); Cerro Juárez, 8 km al NE de Vizarrón, 11 may. 1978, *Zamudio 2822* (IEB ejemplar estéril).

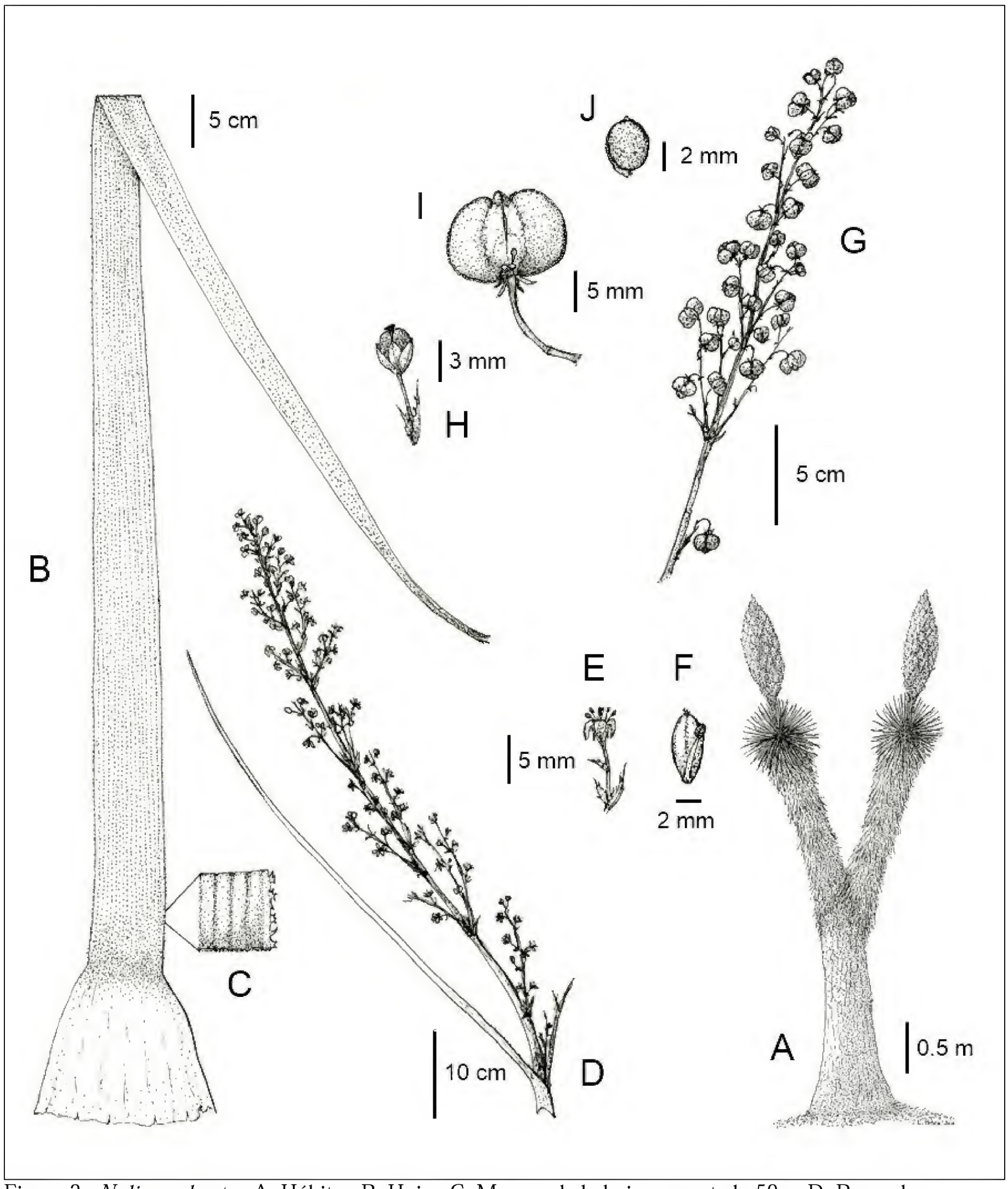

Figura 3. *Nolina robusta*. A. Hábito. B. Hoja. C. Margen de la hoja aumentado 50x. D. Rama de inflorescencia masculina. E. Flor estaminada con bráctea en el artículo del pedicelo. F. Tépalo con estambre. G. Rama de inflorescencia femenina. H. Flor pistilada. I. Fruto. J. Semilla con hilum. Ilustración por el autor.

Elemento que crece en la Sierra Madre Oriental y en la Sierra del Doctor en el noreste y centro de Querétaro, y en el suroeste de San Luis Potosí, en matorrales rosetófilos y en bosques de encino y de coníferas, sobre suelos derivados de calizas. En altitudes entre los 2000 y 3000 msnm. Presenta flores de marzo a mayo y frutos de mayo a julio. Dado que esta especie tiene una distribución restringida, se considera en riesgo para su conservación.

Ruiz-Sánchez & Sprecht (2014) analizaron poblaciones consideradas como *Nolina parviflora*, encontrando que, utilizando marcadores moleculares, los haplotipos de los que se propone como *N. robusta* son diferentes de las entidades del complejo *N. parviflora* en la Faja Volcánica Transmexicana. Por otro lado, debido a su hábito, esta especie podría confundirse con lo que han llamado *N. hibernica* Hochstäter & Donati, pero *N. robusta* tiene los ápices de las hojas erectos o poco curvados, el ancho de la hoja no llega a 4 cm y sus flores son mayores a 2.5 mm de diámetro (Tabla 1). Finalmente, debe aclararse que la colecta de muestras de plantas de este grupo no es fácil y en ocasiones los ejemplares de herbario solo cuentan con brácteas de la inflorescencia que a pesar de su coloración más pálida y de las bases casi paralelas con los márgenes de la hoja, se pueden confundir con hojas y dificultan la identidad de la especie. Sin embargo, con características de la inflorescencia, flores o frutos puede determinarse la especie con más seguridad (ver clave de identificación y cuadro 1).

En San Luis Potosí, se registra el nombre local de "soyate" para esta especie con las flores comestibles y las hojas utilizadas para hacer escobas y abanicos.

Clave de identificación de las especies nuevas y de dos cercanamente relacionadas

1. Brácteas de inflorescencia menores a 30 cm de largo, flores pistiladas 4–8/ nudo, base de óvulos no engrosadas ..... **Nolina parviflora**

1. Brácteas de inflorescencia mayores a 40 cm de largo, flores pistiladas 1–4/ nudo, base de óvulos engrosadas.

2. Hojas menores a 2 cm de ancho, flores estaminadas 4/ nudo, brácteas de inflorescencia menores a 45 cm de largo, frutos casi igual de largo que ancho, semillas 4–5 mm de largo ..... **Nolina orbicularis**

2. Hojas mayores a 2.5 cm de ancho, flores estaminadas 2/ nudo, brácteas de inflorescencia mayores a 50 cm de largo, semillas 3–4 mm de largo, frutos más anchos que largos.

3. Hojas con ápices curveados, enteros, ramas de inflorescencia divaricadas, flores estaminadas de 2 mm de diámetro, flores pistiladas 1(2)/ nudo, base de óvulos ligeramente engrosada, margen de lóbulos de frutos aparente y grueso ..... **Nolina hibernica**

3. Hojas con ápices rectos, desintegrándose en fibras, ramas de inflorescencia erectas a adpresas, flores estaminadas de 2.5 mm de diámetro, flores pistiladas 2–4/ nudo, base de óvulos muy engrosada, sin margen en lóbulos de frutos o éste apenas conspicuo ..... **Nolina robusta**

Caracteres	N. parviflora	N. orbicularis	N. robusta	N. hibernica
Marcescencia	Cerca de las rosetas, deprimidas a descendentes	Cerca de las rosetas, depresas a descendentes	A lo largo de rama o tallo depresas	A lo largo de ramas, descendentes
Largo de hojas	100–150 cm	67–92 cm	70–130 cm	120 cm

Ancho de hojas	1–2 cm	1.4–1.6 cm	2.5–4 cm	4 cm
Ápice de hoja	Recto a algo curveado con fibras	Recto sin fibras, algo curveado en las jóvenes	Recto con fibras	Ampliamente curveado sin fibras
Color margen	Verde amarillo a marrón con la edad	Amarillo a marrón con la edad	Amarillo a marrón con la edad	Marrón a rojizo con la edad
Largo inflorescencia	2–2.5 m	2 m	2.5 m	1.4 m
Largo de brácteas	Hasta 30 cm	Hasta 43 cm	Hasta 50 cm	Hasta 61 cm
Ramas inflorescencia	Adpresas	Divaricadas a difusas	Adpresas a erectas	Divaricadas
Flores estaminadas por nudo	2	4	2	2
Pedicelos de flores estaminadas	3–4 mm articulación cerca de la base	4–5 mm articulación cerca de la base	3–4 mm articulación cerca de la de la mitad (con bractéola)	4–5 mm articulación abajo de la mitad
Diámetro de flores estaminadas	3–3.5 mm	2 mm	2–2.5 mm	2 mm
Flores pistiladas por nudo	4–8	2–4	2–4	1(2)
Pedicelos en frutos	7–12 mm	6–8 mm articulación a 1/3 de la base	6–8 mm articulación a 1/3 de la base	8–10 mm articulación a 1/3 base
Base de óvulos	Sin engrosamiento	En forma de repisa a globosa	En forma de repisa o callo	Engrosamiento ligero
Largo de frutos	6–10 mm	8–9 mm	8–9 mm	6.5–8 mm

Ancho de frutos	10–14 mm	9–10 mm	10–11 mm	8–10 mm
Margen en lóbulos de frutos	Presente	Presente	Ausente o muy delgado	Presente, muy grueso
Hendidura de fruto	2 mm	2–3 mm	3 mm	2–3 mm
Largo de semilla	3–4 mm	4–5 mm	3 mm	3.5–4 mm
Ancho de semilla	3–3.5 mm	3–4 mm	2 mm	2–2.5 mm
Testa de semilla	Marrón-rojiza	Marrón claro	Marrón-rojiza	Marrón oscura

Tabla 1. Comparación entre las especies nuevas y *Nolina parviflora* y *Nolina hibernica*. Información de ejemplares de herbario y literatura (Hemsley 1884; García-Mendoza 2010; Hochstätter & Donati 2010).

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TAXONOMY OF THE *AMSONIA TABERNAEMONTANA* COMPLEX (APOCYNACEAE: RAUVOLFIOIDEAE)

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ABSTRACT

The *Amsonia tabernaemontana* complex for the forthcoming treatment of *Amsonia* in the Flora of North America will be treated as a single species with four geographically and morphologically intergrading varieties: var. *tabernaemontana*, var. *salicifolia*, **Amsonia tabernaemontana** var. **illustris** (Woodson) J.K. Williams, **comb. et stat. nov.,** and **Amsonia tabernaemontana** var. **repens** (Shinners) J.K. Williams, **comb. et stat. nov.** *Amsonia salicifolia* var. *ciliolata* A. DC. is lectotypified. A key to the varieties of *A. tabernaemontana* is provided.

Amsonia tabernaemontana Walt. is a widespread species found throughout the temperate forest of the southeastern USA and is recognized within the genus by its glabrous elliptic leaves, flat stigmatic head, and pubescent corolla tube. Two additional species of *Amsonia* distributed throughout the southeastern USA also have a flat stigmatic head and a pubescent corolla tube: *Amsonia illustris* Woodson and *A. repens* Shinners. These two species have been distinguished from *A. tabernaemontana* chiefly by having pubescent vs. glabrous sepals.

When Woodson (1929) described *Amsonia illustris* he recognized its similarity to *A. tabernaemontana* var. *gattingeri* Woodson, noting that both taxa have linear-lanceolate leaves, pubescent corolla tubes, and a dense inflorescence. He distinguished *A. illustris* from var. *gattingeri* by only one character –– a pubescent vs. glabrous calyx. Woodson (1938) subsequently synonymized var. *gattingeri* under var. *salicifolia* (Pursh) Woodson. Shinners (1951) described a second species of *Amsonia* with a pubescent corolla and calyx, *A. repens* Shinners, which he considered similar to *A. illustris* based on its pubescent corolla and calyx but distinct from it based on its smaller leaves and creeping/geniculate rootstock.

Herbarium, type, and field observations of *Amsonia illustris*, *A. repens*, and *A. tabernaemontana* throughout their ranges (Fig. 1) necessitate a reevaluation of their taxonomic status. Chief among these is the discovery of populations that have discontinuous variation in calyx vestiture. Field trips in Texas encountered populations of *A. tabernaemontana* with individual stems with an inflorescence of flowers with glabrous calyces growing from the same rootstock as individual stems having an inflorescence of flowers with pubescent calyces. Consequently, calyx vestiture in *A. tabernaemontana* appears to be a character that does not merit utilization in species diagnosis. Among herbarium collections from along the border of Indiana and Missouri (Fig. 1) are other populations of *A. tabernaemontana* where individuals with pubescent sepals exist with individuals with glabrous sepals.

In their description of *Amsonia tabernaemontana* Correll & Johnston (1970) noted the following:

> "This species along with… *A. illustris*, and *A. repens*, form an extremely close alliance, and it is questionable as to whether or not they should be maintained as separate species rather than variants of one complex unit. The degree of pubescence or lack of pubescence on the… calyx, that mainly separate these entities, is not an entirely reliable characteristic."

My observations of *A. tabernaemontana* throughout its range (Fig. 1) agree with Correll and Johnston –– *A. illustris*, *A. repens*, and *A. tabernaemontana* should be treated as "variants of one complex unit" where calycine vestiture is treated as a clinal characteristic gradually increasing in appearance with the western distribution of *A. tabernaemontana*.

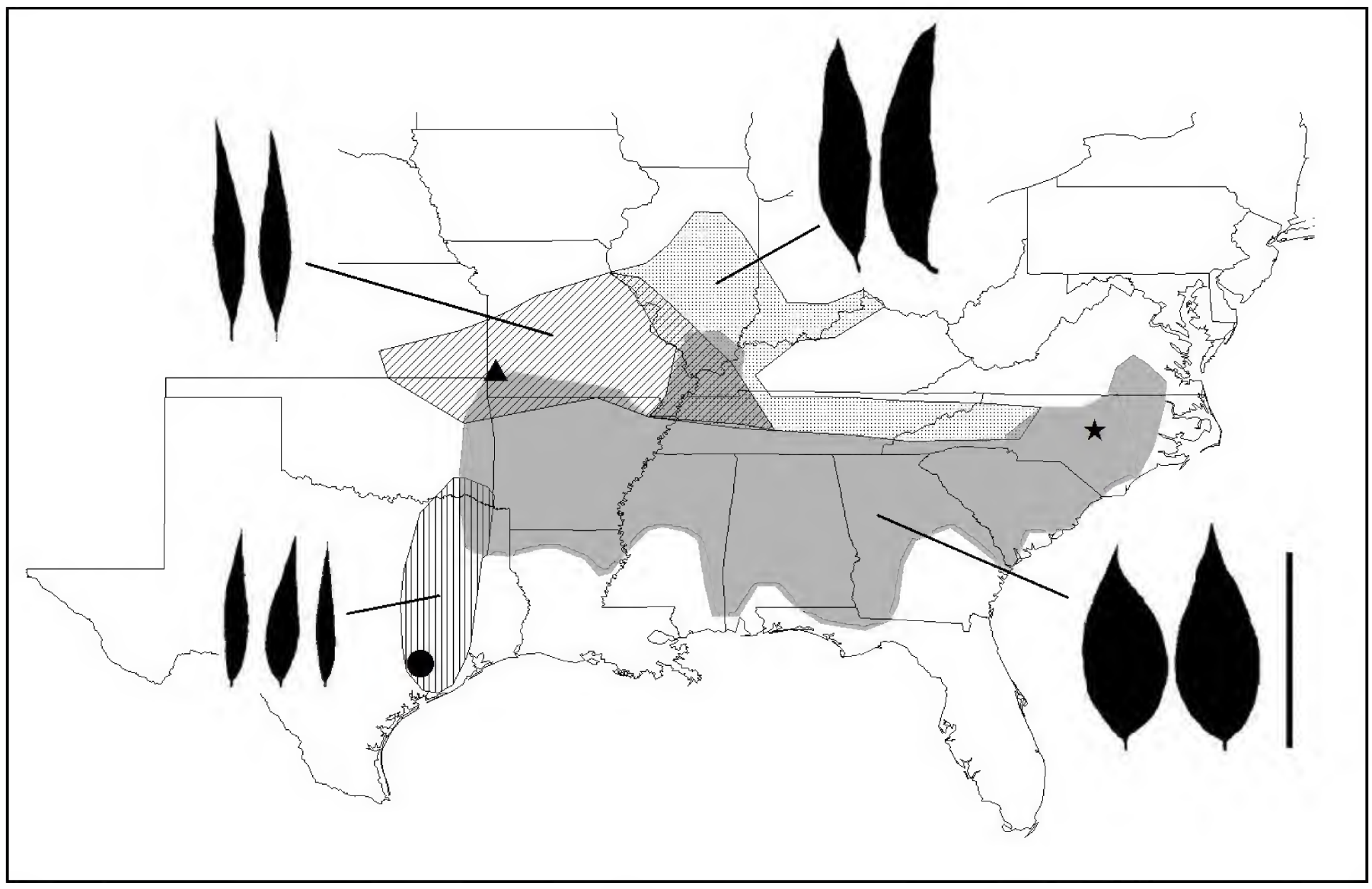

Figure 1. *Amsonia tabernaemontana* complex. Var. tabernaemontana (gray shaded, generalized type locality star). Var. salicifolia (square hatching, type locality unknown). Var. illustris (crosshatch, type locality triangle). Var. repens (horizontal hatching, type locality circle). Leaf scale bar represents 10 cm. Areas of overlap represent populations where variation in character states used to identify the taxa occur.

In the eastern part of its range *Amsonia tabernaemontana* has a sparse inflorescence (Fig 2) and elliptic leaves (Fig 1), but as the species approaches central Tennessee the leaves become progressively lanceolate (Fig. 1) and the inflorescence more compact and dense (Fig 2), while the calyx remains glabrous. Variants with these characters correspond to var. *salicifolia* (Pursh) Woodson. Toward the border of Missouri and Indiana, plants of *Amsonia* that have been traditionally recognized as both *A. tabernaemontana* and *A. illustris* begin to appear in the same populations. These populations are recognized by the presence of individuals with pubescent calyces and individuals with glabrous calyces. Leaf shape is mostly lanceolate within these populations. Within the Ozark Plateau of Missouri the populations of *Amsonia* with pubescent corolla tubes are exclusively individuals with lanceolate leaves and pubescent calyces. Likewise towards the southern portion of its range along the Texas/Oklahoma border, individuals of *Amsonia* with pubescent calyces (*A. repens*) and individuals with glabrous calyces (*A. tabernaemontana*) are found within the same population and, as mentioned above, occasionally growing from the same rootstock. Further south into Texas through the Blackland Prairies towards the Gulf Coast, the populations of *Amsonia* with pubescent corolla tubes are exclusively with lanceolate leaves and a pubescent calyx.

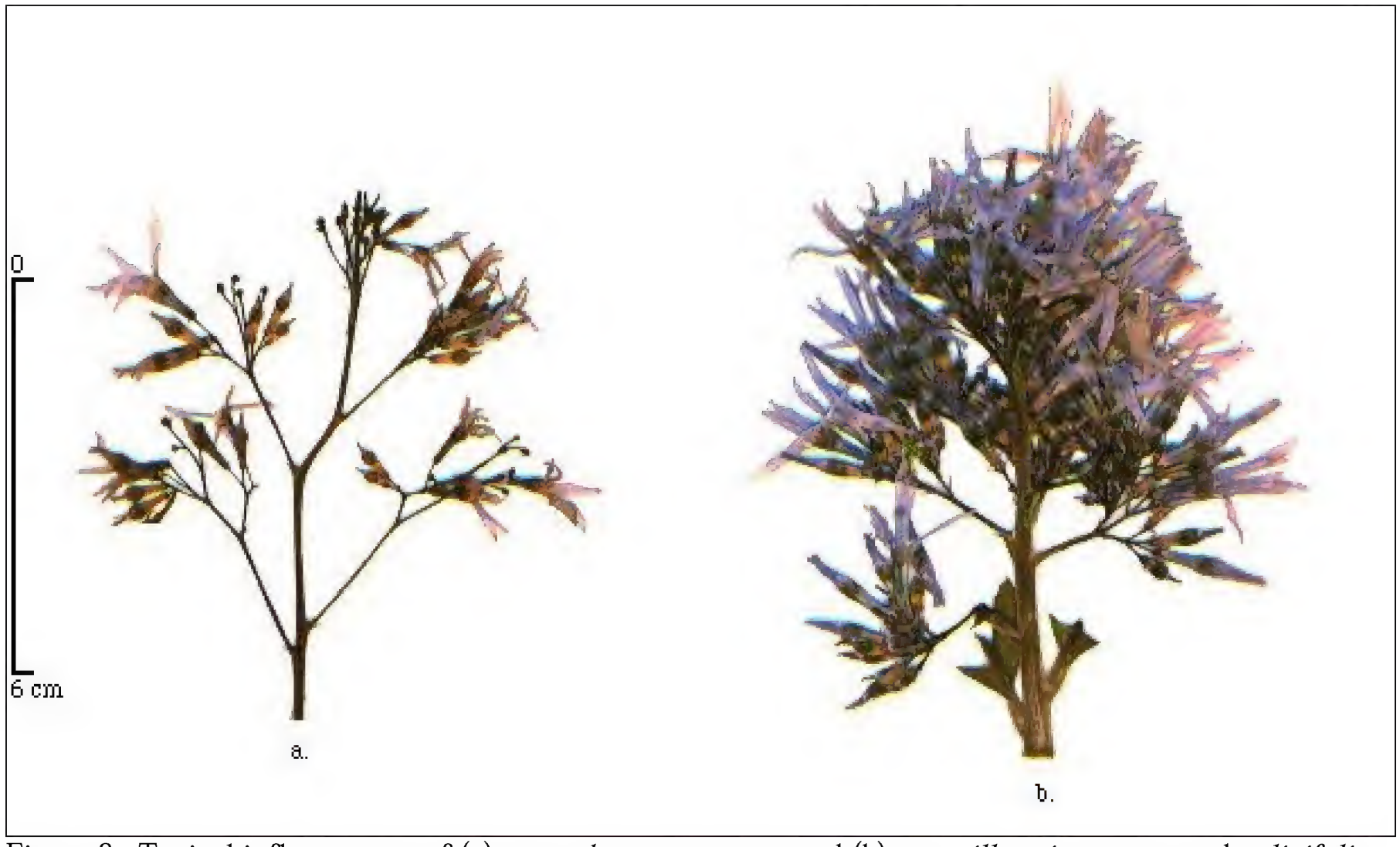

Figure 2. Typical inflorescence of (a) var. *tabernaemontana* and (b) vars. *illustris*, *repens*, and *salicifolia*.

Because *Amsonia illustris*, *A. repens*, and *A. tabernaemontana* are the only taxa of *Amsonia* that have a pubescent corolla tube, and because the taxa share a continuous distribution throughout the Southeastern United States (Fig. 1), the taxa are here viewed as similar "entities that intergrade over… regions of contact (Turner and Nesom 2000). Consequently, the taxa are here treated as variants of the same species. Subsequently, it is here proposed that *A. illustris* and *A. repens* be treated as varieties of *Amsonia tabernaemontana*. The new combinations are here made.

Key to the varieties of *Amsonia tabernaemontana*

1. Leaves ovate to oblong-elliptic; inflorescence loose, below to barely rising above the leaves, of 15-50 flowers; calyx glabrous; fruits 1-4 pairs per inflorescence ..... var. **tabernaemontana**
1. Leaves narrowly elliptic to linear-lanceolate; inflorescence in compact cluster, ascending above the leaves, from 50-80 flowers; calyx glabrous to pubescent; fruits 5-10 pairs per inflorescence.
2. Calyx glabrous ..... var. **salicifolia**
2. Calyx pubescent.
3. Calyx ciliate, hairs emerging from the margins and or body of the calyx lobes, calyx tube glabrous (Fig 3); adaxial leaf midrib glabrescent; leaves 7-10 cm long; Ozark plateau and the Central forest/grassland transition zone ..... var. **illustris**
3. Calyx tomentose, hairs emerging from the calyx tube, calyx lobes glabrous (Fig 3); adaxial leaf midrib villous; leaves 5-7 (9) cm long; Texas Blackland Prairies to the Gulf Coast Prairie ..... var. **repens**

AMSONIA TABERNAEMONTANA Walt., Fl. Carol. 98. 1788. **NEOTYPE** (Ward 2008): **South Carolina**. Darlington Co.: 3 Jun 1941, *B. Smith* 1114 (USCH!;). Detailed discussion on the selection of type in Ward (2010).

A. **Amsonia tabernaemontana** var. **tabernaemontana**

Anonymus suffrutex Gronov., Fl. Virg. 26. 1739. **TYPE**: **Virginia**. No collection data, *J. Clayton 306* (holotype: BM-Clayton Herbarium, not located, presumed lost Pringle (2004); Reveal & Jarvis 2009; Ward 2010).

Tabernaemontana amsonia L., Sp. Pl. ed. 2. 1: 308. 1762. *Tabernaemontana humilis* Salisb., Prodr. Strip. Chap. Allerton. 148. 1796. *Amsonia amsonia* (L.) Britton, Mem. Torrey Club 5: 262. 1894. **LECTOTYPE** (Reveal & Jarvis 2009): No collection data (LINN 304.5!).

Amsonia latifolia Michx., Fl. Bor. Amer. 1:121. 1803 ≡ *Ansonia latifolia* (Michx.) Raf., New Fl. 4:58. 1838. **TYPE**: In umbrosis humidis sylvarum Carolinae, *Michaux s.n.* (holotype: P!).

Amsonia tristis Smith in Rees, Cycl. 35: Amsonia No. 2. 1817. **TYPE**: **England**. London, from the garden of James Vere at Knightsbridge, Jun 1808, *J. Vere s.n.* (holotype: LINN-HS 449.23!).

Amsonia salicifolia Pursh var. *ciliolata* A. DC., Prodr. 8:385. 1844. **LECTOTYPE** (designated here): **Louisiana**. 1836, *L.F. Tainturier s.n.* (G-DC 136584/1!). Candolle (1844) cited two specimens -- one was collected in Alabama by Torrey, and the other specimen was collected in Louisiana by Tainturier. The Tainturier specimen was selected as the lectotype because the Torrey specimen was not been located by Williams in either G or P.

Var. *tabernaemontana* is recognized by its elliptic-oblong leaves, sparse inflorescence (Fig. 2), and distribution throughout the southeastern USA (Fig 1). It is often found with glabrous stems, but a few populations in South Carolina (Colleton, Dorchester, Laurens, McCormick, and Saluda counties) have pubescent stems. Pringle (2004) and Ward (2010) have given detailed accounts of the nomenclatural history of this species.

In his treatment of the Apocynaceae, de Candolle (1844) recognized *Amsonia salicifolia* and described a new variety for the species: var. *ciliolata* A. DC. Var. *ciliolata* was described as identical to var. *salicifolia* with the exception of having ciliolate versus glabrous leaves. This taxon has subsequently been identified as *A. ciliata* var. *ciliolata* (A. DC.) Lemke & Ayers in two publications (Smith et al. 1992; Hyatt 1993) but in neither publication was the basionym cited. In accordance with Article 41.1 of the Melbourne Code (McNeill et al. 2013), the name is not valid. Examination of the type specimen clearly indicates it to be a specimen of var. *tabernaemontana*.

B. **Amsonia tabernaemontana** var. **salicifolia** (Pursh) Woodson, Ann. Missouri Bot. Gard. 15: 406. 1928. *Amsonia salicifolia* Pursh, Fl. Amer. Sept. 184. 1814. *Amsonia salicifolia* (Pursh) Raf., New Fl. 4: 58. 1838. *Amsonia tabernaemontana* var. *salicifolia* (Pursh) Woodson ex Máthé & Máthé, Bot. Közlem. 69: 148. 1982. **TYPE**: North America, May, *Lyon s.n.* (not located, Ewan 1979).

Amsonia tabernaemontana var. *gattingeri* Woodson, Ann. Missouri Bot. Gard. 15: 408. 1928. **TYPE**: **Tennessee**. Knox Co.: Islands in Cumberland River, near Nashville, Jun, *Gattinger 2268* (holotype: MO!; isotype: GH!).

Diagnostic characters used to define var. *salicifolia* have varied, probably because none of the previous monographers of *Amsonia* (Woodson 1928, 1938; Máthé & Máthé 1982) ever cited, located, or observed the type specimen of var. *salicifolia*.

In his original description of *Amsonia salicifolia*, Pursh (1814) described the species as smooth having linear-lanceolate leaves, acute at both ends. He cited "In Carolina and Georgia, Lyon, May" as the type description. The "Lyon" in the type description refers to John Lyon (1765-1814),

noted nurseryman and botanical explorer of the American East Coast (Ewan & Ewan 1963). In 1979 Pursh's *Flora Americae Septentrionalis*, where *A. salicifolia* was originally described, was reissued as a facsimile reprint. In the reprint, Ewan (1979) included a list of the type specimens for all the names described by Pursh. For *A. salicifolia*, Ewan (1979) simply wrote "not located."

In the first thorough monograph of *Amsonia*, Woodson (1928) treated *A. salicifolia* as a variety of *A. tabernaemontana*, creating the new combination *A. tabernaemontana* var. *salicifolia* (Pursh) Woodson. Woodson regarded the taxa conspecific based on their shared pubescent corollas and glabrous follicles. He distinguished the two varieties using leaf morphology, var. *tabernaemontana* with ovate to oblong-lanceolate leaf blades, and var. *salicifolia* with lanceolate to linear-lanceolate leaf blades. Woodson (1928) also described a third variety of *A. tabernaemontana*, var. *gattingeri* Woodson. He defined var. *salicifolia* and var. *gattingeri* as both having lanceolate to linear-lanceolate leaf blades. He distinguished the two varieties by their inflorescence morphology, with var. *salicifolia* having a sparse inflorescence and var. *gattingeri* having a dense inflorescence. Woodson (1938) subsequently expanded his concept of var. *salicifolia* to include a dense inflorescence when he synonymized var. *gattingeri* under var. *salicifolia*. Correll and Johnston (1970) followed Woodson's (1938) treatment and recognized var. *gattingeri* as a synonym of var. *salicifolia*. However, in the most recent treatment of the *A. tabernaemontana* complex, Máthé & Máthé (1982) recognized var. *salicifolia* and var. *gattingeri* as distinct from one another, using the same "sparse" vs. "dense" inflorescence criterion.

As recognized here, the concept of var. *salicifolia* follows Woodson's (1938) diagnosis, where he defined the taxa as having lanceolate to linear-lanceolate leaf blades, dense inflorescence, and glabrous calyces.

In his original description of *Amsonia salicifolia*, Pursh (1814) reported its distribution as "Carolina and Georgia." Although lanceolate- to linear-lanceolate-leaved specimens occur sporadically throughout the American Southwest, the distribution of var. *salicifolia* is centered in Tennessee, Illinois, and Indiana (Fig. 1).

C. **Amsonia tabernaemontana** var. **illustris** (Woodson) J.K. Williams, **comb. et stat. nov.** *Amsonia illustris* Woodson, Ann. Missouri Bot. Gard. 16: 407. 1929. **TYPE**: **Missouri**. Jasper Co.: Gravelly beds near Webb City, 15 Jul 1909, *E. J. Palmer 2438* (holotype: MO!).

Vars. *illustris* and *repens* might appear synonymous given that they both possess pubescent calyces and lanceolate leaves, and the smaller leaves and geniculate rootstock described by Shinners (1951) to separate the taxa are not consistent characters. However, while both taxa possess pubescent calyces, the distribution of their pubescence is not similar. Observations of several hundred herbarium specimens reveal that the sepal hairs of var. *illustris* are ciliate, emerging from the margins of the calyx lobes (Fig 3a), and occasionally from the body of the calyx lobe, while the sepal hairs of var. *repens* are tomentose and emerge from the calyx tube (Fig. 3b). The calyx lobes themselves are glabrous. Although a nuanced character the difference between the two taxa is consistent with the geographic distinction of var. *illustris* and var. *repens* (Fig. 1). Observations also indicate that the adaxial leaf midrib of var. *repens* is consistently villous, while in var. *illustris* the midrib is glabrous to glabrescent.

D. **Amsonia tabernaemontana** var. **repens** (Shinners) J.K. Williams, **comb. et stat. nov.** *Amsonia repens* Shinners, Field & Lab. 19: 126. 1951. **TYPE**: **Texas**. Wharton Co.: 2 mi W of El Campo along Hwy 59, infrequent in pasture adjoining highway, 29 Mar 1949, *Cory 55089* (holotype: SMU!).

Figure 3. Scanning electron microscopy photograph of the calyx of (left) var. *illustris* and (right) var. *repens*. The images were taken at 64x using 30Kv by the author. The scale bar equals 10 mm.

Amsonia repens Shinners was previously treated as a variety of *A. tabernaemontana* in Turner et al. (2003). Unfortunately, when Turner et al. (2003) proposed the new combination they did not reference the basionym. Article 41.1 of the Melbourne code (McNeill et al. 2013) states that new combinations are not validly published unless "accompanied by a reference to the basionym." The variety is here validly published with the inclusion of its basionym.

As described above, var. *repens* is distinguished from var. *illustris* by the distribution of the calyx hairs (calyx tube vs. calyx lobes) and its distribution (Fig. 1) in southern Oklahoma and Texas (vs. northern Oklahoma and Missouri).

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PANIC GRASSES OF SOUTHEASTERN MISSOURI –– ONE NEW AND ONE REDISCOVERY

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ABSTRACT

Documentation is provided for *Dichanthelium dichotomum* subsp. *roanokense* as new to the flora of Missouri (Scott and Stoddard counties) and for the rediscovery of *Dichanthelium dichotomum* subsp. *yadkinense* in the state (previously known from Reynolds Co., rediscovered in Stoddard Co.). Both taxa occur in the Mississippi Embayment area.

In 2016, while conducting routine identifications and reviewing specimens filed as *Dichanthelium dichotomum* (L.) Gould in the Missouri Botanical Garden Herbarium (MO), several unusual specimens were encountered and are evidence of the rare occurrence of two taxa in Missouri. The names used here follow the taxonomy of Flora of North America (Freckmann & Lelong 2003). Both taxa, however, are treated at species rank by LeBlond (2017), which is reasonable considering that their broad sympatry extends into Missouri.

New to the Missouri flora

Dichanthelium dichotomum subsp. *roanokense* (Ashe) Freckmann & Lelong (= *Dichanthelium roanokense* (Ashe) LeBlond) occurs on the coastal plain from Delaware to southeastern Texas and in the West Indies. This subspecies "grows in marshes, wet pinelands, wet woods, and the borders of swamps, a relatively uncommon subspecies" (Freckmann & Lelong 2003). It was not included in the flora of Missouri (Yatskievych 1999), but its discovery in swamps of the Mississippi Embayment of Missouri was expected. Subsp. *roanokense* is distinct in its lack of bearded nodes and its relatively small spikelets.

Specimens examined. **Missouri**. Scott Co.: Locally common in swale of sand prairie, T28N, R14E, S27, SW4 Charleston Baptist Church Camp, on S side of State Hwy 77 ca. 3 mi SE of Interstate 55 exit in Benton, 12 Jul 2002, *Laatsch s.n.* (MO). Stoddard Co.: Otter Slough Conservation Area along extension of County Rd 686 about 50 meters W of parking area, Powe Quadrangle, T24N, R9E, SE, SE, Sec. 8. 36.73197° N, 90.10150° W, caespitose, in dried-down disturbed wetland between extension of County Rd 686 and flatwood forest, with *Spiranthes praecox*, *Dichanthelium scoparium*, *Festuca paradoxa*, *Steinchisma hians*, *Juncus biflorus*, *J. brachycarpus*, and *J. effusus*, 13 Jul 2014, *Brant 7646* (LINU, MO).

Rediscovery of *Dichanthelium dichotomum* subsp. *yadkinense*

Dichanthelium dichotomum subsp. *yadkinense* (Ashe) Freckmann & Lelong (= *Dichanthelium yadkinense* (Ashe) Mohlenbrock; treated as *Panicum dichotomum* var. *yadkinense* (Ashe) Lelong in Yatskievych 1999) was collected from an acid gravel-wash community on 30 May 1992 at Johnson's Shut-Ins State Park, Reynolds Co., Missouri (Heumann 1993). This population and the site were destroyed by the Ameren Power Company's dam failure above Johnson's Shut-Ins State Park. Attempts to relocate populations near the original site have failed. A second collection, documented here, confirms the existence of subsp. *yadkinense* in southeastern Missouri. Subsp. *yadkinense* has bearded lower nodes and larger spikelets.

Specimen examined. **Missouri**. Stoddard Co.: Otter Slough Conservation Area N and NE of headquarters area. T24N, R9E, Central area Sec. 17, Powe Quadrangle, caespitose, in overflow woods, 16 Sep 2001, *Brant 4787* (MO).

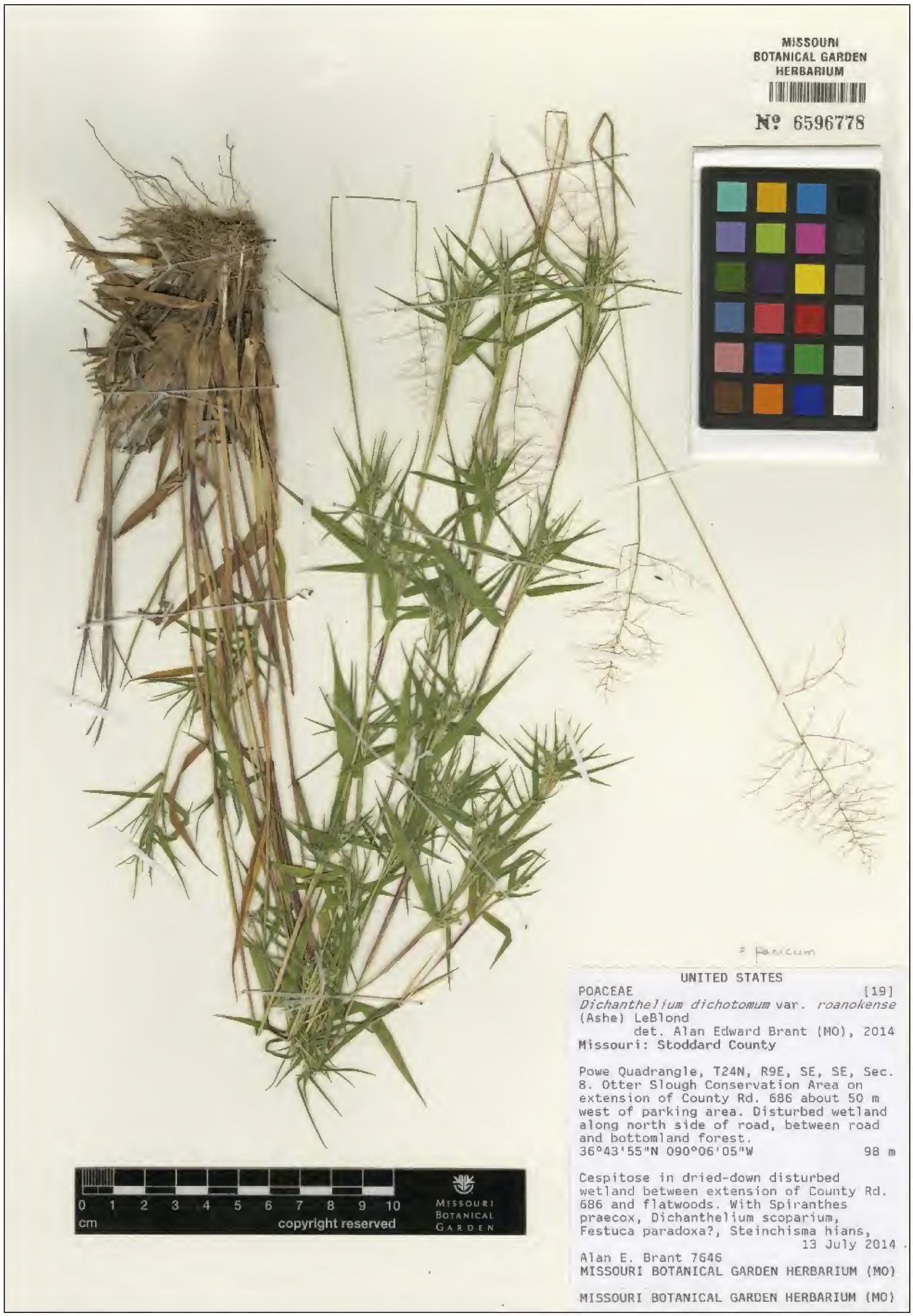

Figure 1. *Dichanthelium dichotomum* subsp. *roanokense*. *Brant 7646* from Stoddard County. Missouri Botanical Garden Herbarium imaging lab.

Dichanthelium dichotomum subsp. *yadkinense* occurs in much the same habitats and has a similar distribution as subsp. *roanokense* (Freckmann & Lelong 2003) and was expected in similar old coastal plain habitats in Missouri. Its presence in an acid gravel-wash community in the St. Francois Mountains of Missouri (Reynolds Co., as reported by Heumann 1993) is unusual. There are two recent anecdotal reports of collections (J.R. Thomas & Rick Gray, pers. comm. 2018) of this taxon from Missouri, but the collections are not available for examination.

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POTENTILLA JEPSONII VAR. *KLUANENSIS* (ROSACEAE): A NEW VARIETY FROM YUKON AND ALASKA TO WASHINGTON

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ABSTRACT

Potentilla jepsonii var. **kluanensis** Ertter, **var. nov.**, is described for populations referred to as "the montane phase of *P. litoralis*" in *Flora of North America North of Mexico.* The variety is centered in the St. Elias Mountains in southwestern Yukon and adjacent Alaska, with scattered populations in British Columbia, southwestern Alberta, and north-central Washington. The new variety differs from typical *P. jepsonii* in having appressed to ascending (vs. spreading to loosely appressed) petiole hairs and leaflets with more revolute margins; it differs from *P. litoralis* in smaller overall size and alpine habitats; and it differs from both in somewhat shorter pedicels and leaves that are more subpalmate than subpinnate (leaflets on less than distal ¼ of leaf axis) with fewer teeth and whiter abaxial surfaces.

Potentilla sect. *Pensylvanicae* Poeverl. is one of the sections that was significantly revised for *Flora of North America North of Mexico* (Ertter 2008; Ertter et al. 2015). Six separate species were recognized, most of which had been encompassed in an inclusive *P. pensylvanica* L. in previous floristic treatments at one time or another (e.g., Cody 1996; Hitchcock et al. 1961; McGregor 1986). One of these, *Potentilla jepsonii* Ertter, is a *nomen novum* for *P. pensylvanica* var. *ovium* Jepson, with the epithet changed at the species rank in order to avoid nomenclatural confusion with the unrelated species *P. ovina* J.M. Macoun, which has an overlapping range.

Although *Potentilla jepsonii* has been included within *P. pensylvanica* (e.g., Ertter 1993; Holmgren 1997; Hitchock et al. 2018), vestiture and leaf dissection (Fig. 1) actually indicate a closer relation to *P. litoralis* Rydb., leading Soják (2006) to provide the combination *P. litoralis* var. *ovium* (Jepson) Soják. *Potentilla litoralis* is otherwise a larger plant that ranges from the north Atlantic coast across the northern Great Plains to Alaska; synonyms include *P. virgulata* A. Nels. and *P. pectinata* Raf. In contrast, *P. jepsonii* is generally a smaller plant restricted to mountain ranges from eastern Oregon to western Montana, south to eastern California and northern Arizona. As stated in Ertter et al. (2015, p. 217), "[*P. jepsonii*] is for the most part well separated geographically and elevationally [from *P. litoralis*]. The exception is the montane phase of *P. litoralis*, which, at the current stage of knowledge, is somewhat arbitrarily delimited from *P. jepsonii* in the northern Rocky Mountains; collections from Waterton Lakes National Park in Alberta and the Okanogan Mountains in Washington are tentatively placed here in *P. jepsonii*."

The aforementioned collections from Alberta and Washington resembled, but apparently were widely disjunct from, the "montane phase of *P. litoralis.*" The latter was primarily represented by a cluster of problematic collections from the St. Elias Mountains of southwestern Yukon that might simply be depauperate *P. litoralis* growing in suboptimal habitats. Fieldwork in June 2017, however,

confirmed that the problematic Yukon plants on montane slopes and ridges are in fact morphologically and ecologically distinct from typical *P. litoralis* that is common on adjacent flatlands, including the receding shoreline of Kluane Lake, roadsides, and other disturbed habitats. Furthermore, several comparable herbarium specimens from mountains in central British Columbia came to light, reducing the disjunction between the Yukon populations and those from Alberta and Washington.

Figure 1. Comparison of basal leaves of *Potentilla pensylvanica* (*Ertter & Töpel 19225,* White Mountains of California), *P. litoralis* (*Ertter 22885*, Kluane Lake Research Station, Yukon), *P. jepsonii* var. *jepsonii* (*Ertter & Töpel 19226,* White Mountains of California), and *P. jepsonii* var. *kluanensis* (*Ertter at al. 22866,* Kluane National Park, Yukon), left to right. Significant variation in leaf size and dissection occurs within each species, but the relative average size and dissection is representative.

The populations referred to as "the montane phase of *Potentilla litoralis*" in Ertter et al. (2015), now including the collections from Alberta and Washington, are here described as a new variety of *P. jepsonii.* Varietal rank within *P. jepsonii* is used because of the intermediate nature of otherwise typical *P. jepsonii* from northeastern Oregon, Idaho, northwestern Montana, and northern Nevada, as discussed below. Alternatively, further study could support all three taxa as varieties of *P. litoralis,* as proposed by Soják (2006). All photographs are by the author. Terminology is as defined and used in Ertter et al. (2015). The terms "subpalmate" and "subpinnate" denote stages on a continuum between strictly palmate and unequivocally pinnate leaves, quantitatively expressed as leaflet-bearing distal fraction of the leaf axis.

POTENTILLA JEPSONII Ertter var. **KLUANENSIS** Ertter, **var. nov.** (Figs. 2–5) **TYPE: CANADA. Yukon.** Kluane National Park, abandoned section of original Alaskan Highway across colluvium at S base of Sheep Mountain (Tachäl Dhäl) ca 300 m N of Tachäl Dhäl Visitor Centre, with *Penstemon gormanii, Artemisia frigida, Erigeron caespitosus,* 61.0164°N 138.5241°W, 790 m, 23 Jun 2017, *Ertter et al. 22866* (holotype: UC; isotypes: BABY, DAO, NY).

Ertter: *Potentilla jepsonii* var. *kluanensis*, var. nov.

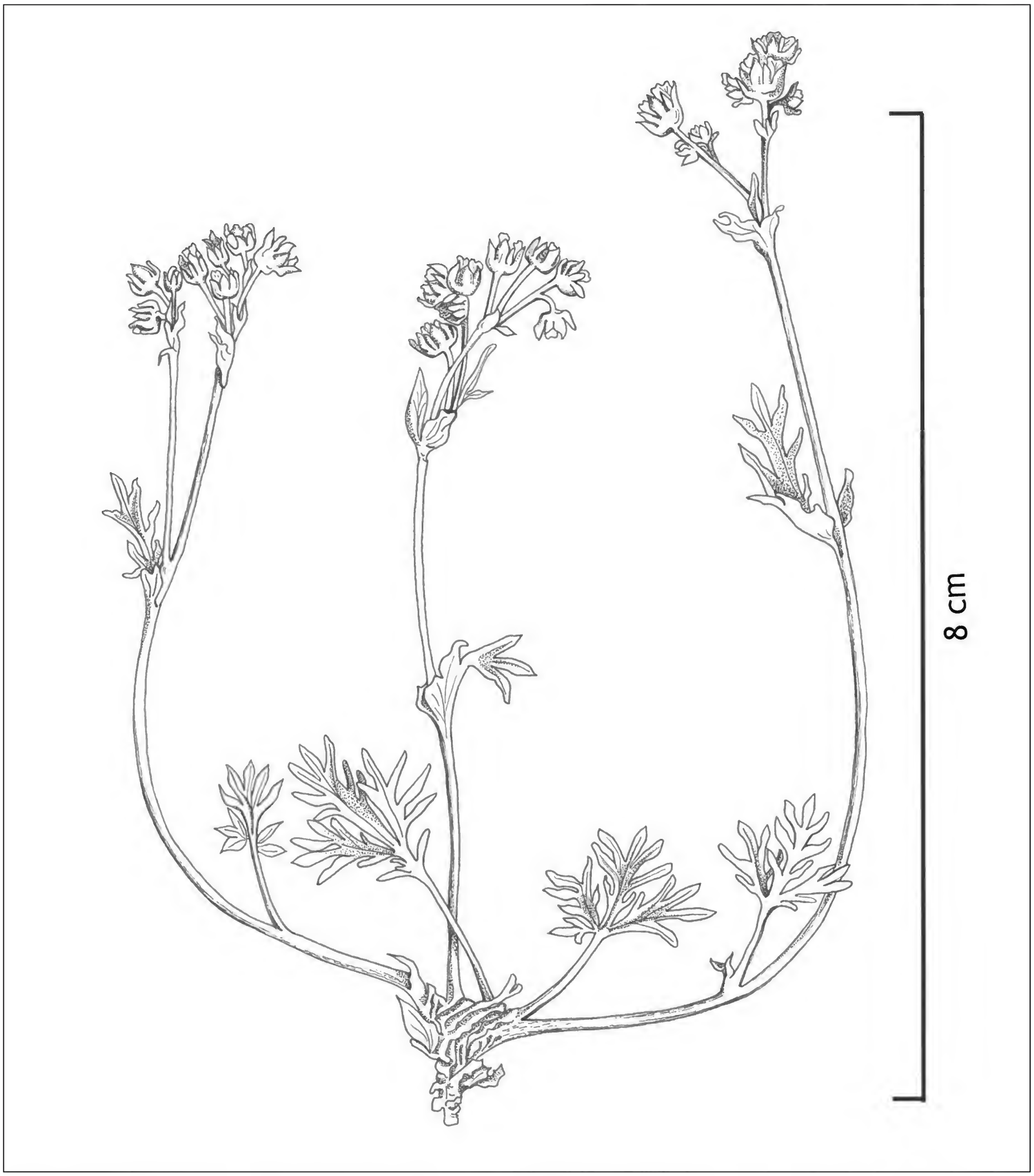

Figure 2. Habit of *Potentilla jepsonii* var. *kluanensis*. Drawing by K. Pappani, based on *Ertter et al. 22866*.

Differs from *Potentilla jepsonii* var. *jepsonii* in having appressed to ascending (vs. spreading to loosely appressed) petiole hairs and leaflets with more revolute margins; differs from *P. litoralis* in smaller overall size, flatter epicalyx bractlets, and alpine habitats; differs from both in somewhat shorter pedicels and leaves that are more subpalmate than subpinnate (leaflets on less than distal ¼ of leaf axis) with fewer teeth and whiter abaxial surfaces. Diagnostic differences are summarized in Table 1.

Plants tufted; caudex branched, sheathed with old leaf bases. **Stems** ascending, 0.5–1.3(–2.3) dm long, 1.5–3 times length of basal leaves. **Basal leaves** subpalmate to subpinnate with distal leaflets ± distinct, 1.5–5(–7.5) cm long; petiole 0.5–2.5(–4.5) cm long, long hairs common to abundant (dense), appressed to ascending, 0.5–1.5 mm long, usually ± stiff, short(/crisped) hairs sparse to common, cottony hairs absent, glands common to abundant; leaflets (1)2(3) per side, on distal 1/6–¼ or less of leaf axis, ± separate, proximal pair separated from others by 1–5 mm of leaf axis, terminal leaflet ± obovate to oblanceolate, 0.8–2 cm × 0.5–1 cm, margins strongly revolute, incised nearly to midvein, undivided medial blade 1–3 mm wide, teeth 2–4 per side, linear (oblanceolate), not overlapping, 2–6(–7) mm × 1–1.5 mm, surfaces dissimilar, abaxial (green) grayish to nearly white, long hairs abundant especially on veins, 0.5–1 mm long, short to crisped hairs (sparse) abundant to dense, cottony hairs absent, glands common to abundant, though often obscured. **Cauline leaves** 1–3. **Inflorescences** 2–14-flowered, congested, scarcely opening in fruit. **Pedicels** 0.1–0.3 cm (proximal to 0.6 cm) long. **Flowers** cup-shaped; hypanthium (pressed) 2.5–4.5 mm diam., ± 1–1.5 mm deep; epicalyx bractlets flat, linear to narrowly elliptic or lanceolate, 2–3.5 × 0.4–1(–1.3) mm, ⅔–¾ times length of sepals; sepals 2.5–4 mm long, apex bluntly acute, abaxial surface sparsely to moderately straight-hairy, abundantly and visibly glandular; petals yellow, lacking darker basal patch, 3–4.5 × 2.5–3.5(–4) mm, ± as long as sepals; filaments ± 1–2 mm long (those opposite sepals longest), anthers 0.3–0.5 mm long; carpels ca 20–50, styles ± 1.2 mm long tapered, papillate-swollen in proximal ± ¾, especially so in proximal ⅓, distal ⅓ often columnar. **Achenes** 1.1–1.3 mm long, smooth, not carunculate.

Flowering from June to July, or to August in Waterton Lakes National Park. Dry colluvium and talus slopes, alpine summits, ridges, and tundra; elev. 790–2500 m (lowest in Yukon, highest in Waterton Lakes National Park).

Other collections examined. CANADA. Alberta. Alpine summit of Sofa Mt., Waterton Lakes National Park, 6 Aug 1953, *Breitung 17206* (UC). **British Columbia.** Mt. Moor [N end Shalups Range], middle Blue Cr. below pass, 8 Aug 1957, *Bird 3374* (UBC); Elizabeth Mine NW of Lillooet, 51°00'N 122°25'W, 19 Aug 1971, *Brink s.n.* (UBC); Mt. Sidney Williams, 54°53'37.7"N 125°24'57"W, l7 Aug 2012, *Marr, Wheeler, & Hebda 12-515* (UC, V). **Yukon.** Observation Mtn., 17 Aug 1773, *Douglas & Douglas 7192* (V); Bullion Creek–Sheep Creek plateau ca 10 km NW of the Slims River, 60°03'N 138°43'W, 2 Jul 1975, *Douglas & Douglas 8447* (ALA [mixed collection w/ *P. pensylvanica*], BRY), 61°02'N 138°40'W, *Douglas & Douglas 8464* (V); e slopes Sheep Mt. near Kluane Lake, 18 Jul 1970, *Krajina & Hoefs s.n.* (UBC); Kaskawulsh nunatak, jct n & central arms Kaskawulsh Glacier, 1 Jul–1 Aug 1965, *Murray & Murray 121* (ALA, COLO); terminus of Kaskawulsh Glacier, 60°49'N 138°44'W, 31 Jul 1966, *Murray & Murray 663* (ALA); Steele Glacier and vic., St. Elias Mts, 5-10 Aug 1967, *Murray & Murray 1358* (ALA). **USA. Alaska.** Ridge at confluence of Baldwin & Logan glaciers, Wrangell-St. Elias NP, 60°52.57'N 141°15.20'W, 16 Jul 2003, *Cook & Eklund 4786* (ALA). **Washington.** Okanogan Co.: Hurley Peak, just N of Mt. Chopaka, 23 Jul 1978, *Kruckeberg 6544* (WTU).

Potentilla jepsonii var. *kluanensis* is known primarily from the St. Elias Mountains in southwestern Yukon and adjacent Alaska, with scattered populations documented in British Columbia south to extreme southwestern Alberta and north-central Washington. Existing collections had been previously determined as *P. pensylvanica* and *P. virgulata,* or even *P. bipinnatifida* Douglas ex Hook., *P. drummondii* Lehm., and *P. saximontana* Rydb.

Etymology. Kluane is the Anglicized word derived from Lhù'àän Män: fish, many – lake in the Dene/Athabaskan dialect of Southern Tutchone. Kluane National Park and Reserve in southwestern Yukon is the source of most collections of the new variety, including the type. The park and reserve share the rugged St. Elias Mountains with Wrangell-St. Elias National Park and Preserve and Glacier Bay National Park in Alaska. The name also honors the Lhù'àän Män Ku Dän–the Kluane Lake People.

The park and reserve lie in the traditional territory of the Kluane Lake People, as well as the Champagne and Aishihik First Nations. Kluane Lake, currently the largest lake in the Yukon Territory on the east edge of the park, has an uncertain future due to the recently changed drainage of A'ay Chù (Slims River) resulting from the receding of Kaskawulsh Glacier; the main river that used to feed the lake now takes an alternate (and much shorter) route to the Pacific Ocean.

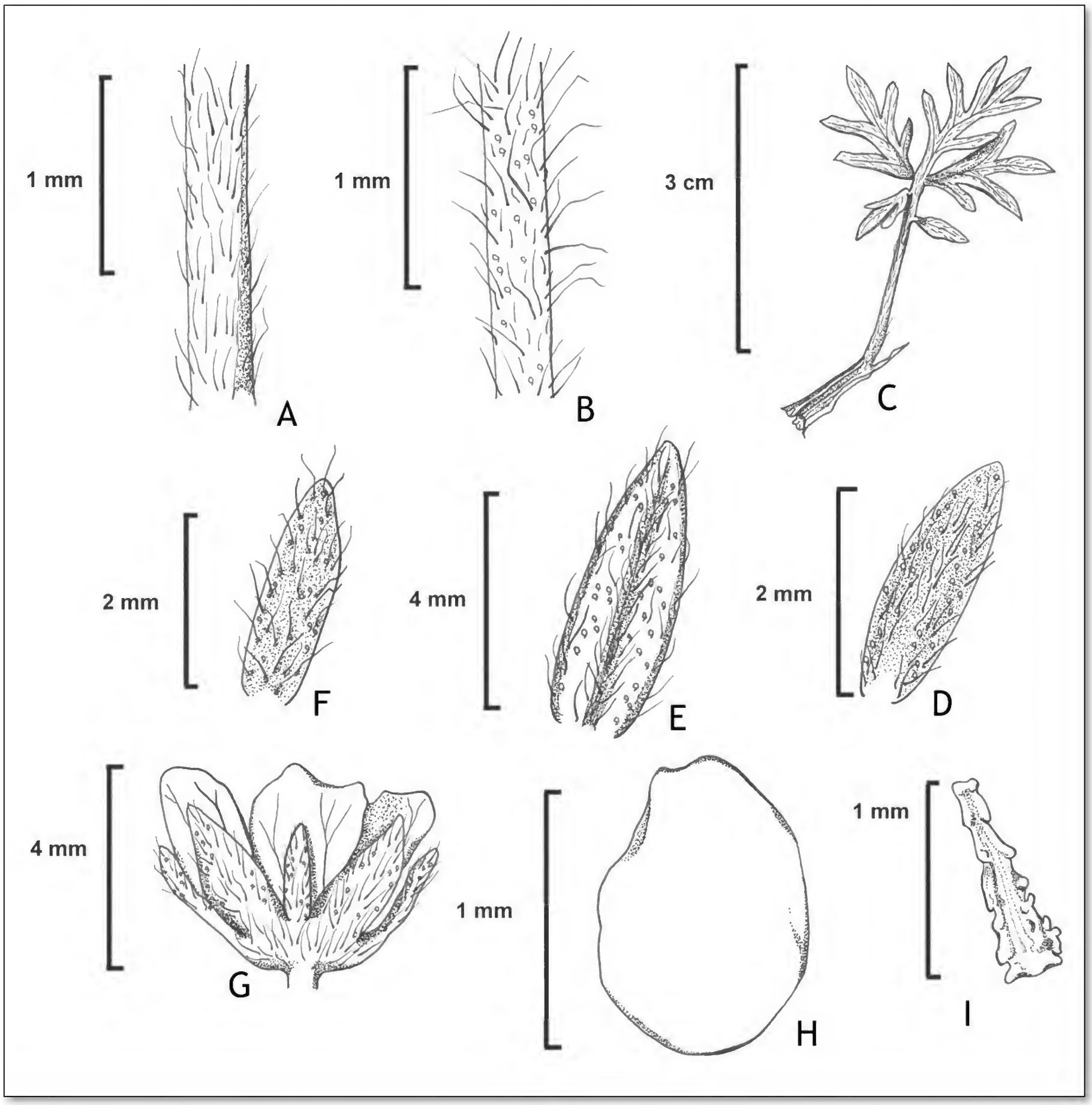

Figure 3. *Potentilla jepsonii* var. *kluanensis* and var. *jepsonii*. A. Hair orientation on petiole of var. *kluanensis*. B. Hair orientation on petiole of var. *jepsonii*. C. Basal leaf of var. *kluanensis*. D. Epicalyx bractlet of var. *kluanensis*. E. Epicalyx bractlet of *P. litoralis*. F. Epicalyx bractlet of var. *jepsonii*. G. Side view of flower of var. *kluanensis*. H. Achene of var. *kluanensis*. I. Style of var. *kluanensis*. Drawings by K. Pappani.

Figure 4. Habitat and habit of *Potentilla jepsonii* var. *kluanensis* at type locality (*Ertter et al. 22866*).

Figure 5. Flower of *Potentilla jepsonii* var. *kluanensis* (left; *Ertter et al. 22866*) compared to significantly larger flower of co-occurring *P. pensylvanica* (right; *Ertter et al. 22867*).

Table 1. Summary of diagnostic differences among *Potentilla litoralis, P. jepsonii* var. *kluanensis*, and *P. jepsonii* var. *jepsonii.* The upper elevational range for *P. litoralis,* adjusted from *Flora of North America North of Mexico* because of the removal of *P. jepsonii* var. *kluanensis,* is based on the type collection of *P. virgulata* from Yellowstone National Park.

	litoralis	**kluanensis**	**jepsonii**
stem length	(0.4–)1–4.5(–6) dm	0.5–1.3(–2.3) dm	(0.2–)0.5–2.6 dm
petiole hair orientation	appressed (ascending)	appressed to ascending	spreading (to loosely appressed)
lflet-bearing distal fraction of leaf axis	1/6–⅓(–½)	1/6–¼ or less	1/6–⅓(–½)
distance separating proximal lflets	2–12(–17) mm	1–5 mm	1–7 mm
terminal lflet length	(1.5–)2–5(–7) cm	0.8–2 cm	(0.5–)1–2.5(–3.5) cm
undivided medial portion of lflet blade	2–10 mm wide	1–3 mm wide	1.5–3(–3.5) mm wide
lflet teeth per side	(2–)5–8	2–4	(2–)3–5(–6)
lflet tooth length/width	2–6	2–6	1.5–4
abaxial leaf color	green to grayish	(green) grayish to nearly white	± grayish, rarely white
pedicel length	0.2–1(–3) cm	0.1–0.3(–0.6) cm	0.2–0.5(–1.2) cm
bractlet curvature	± concave	flat	flat
bractlet/sepal ratio	± ⅔–1	⅔–¾	½–¾
carpel number	50–100	ca 20-50	20–60
elevation	0–2000 m	790–2500 m	(2200–)2500–3700 m

Although the new variety is reasonably distinct both morphologically and ecogeographically from var. *jepsonii* and *P. litoralis,* there are some intermediate and anomalous populations. Plants of *Bennett et al. 17-0574* (BABY, SRP), growing along a path through a spruce-aspen forest halfway between Kluane National Park and Whitehorse, approach var. *kluanensis* morphologically but are more likely to be depauperate *P. litoralis* based on the habitat. In the opposite direction, the single plant of *Caswell 473* (ALA) from along the Slims River is probably an exceptionally vigorous var. *kluanensis* rather than a narrow-toothed *P. litoralis.* Representatives of the intergrade zone between var. *kluanensis* and var. *jepsonii* that have leaflet teeth approaching *kluanense* (revolute, white beneath, linear) but spreading petiole hairs and leaves more subpinnate than subpalmate include *Moseley 512* (ID) from the Lemhi Range of Idaho and *Charlet 8* (UC) from the Jarbidge Mountains of northern Nevada. *Corbin 1767* (CIC) from the Wallowa Mountains of northeastern Oregon has ascending petiole hairs and relatively large flat leaflets approaching those of *P. pensylvanica*, while *Lesica 4052* (MONTU, NY) from the Front Range Mountains of Montana is also transitional to *P. modesta* Rydb.

The preceding collections are all excluded from var. *kluanensis* in large part as a result of giving precedence to appressed to ascending (vs. spreading) petiole hairs as a diagnostic character, since this is the character with the strongest geographic correlation. As a result, *Marr et al. 12-515* (UC, V), from Mt. Sidney Williams in southern British Columbia, is included in the new variety even though the leaflet teeth are not as strongly revolute as most other populations. Intriguingly, collections from the isolated southernmost population of *P. jepsonii* in the San Francisco Peaks north of Flagstaff (e.g., *Ertter et al. 11420* [UC]) are very comparable to *Marr et al. 12*-515 in having appressed-ascending petiole hairs and subpalmate leaves; the optimum disposition of this isolated, anomalous population from Arizona will depend on a more in-depth study of the species complex.

By sheer coincidence, the types of *Potentilla jepsonii* and the new variety are both from Sheep mountains, which provided Jepson's original epithet *ovium* (Jepson 1936). For *P. jepsonii*, this is Sheep Mountain in the White Mountains on the California-Nevada border. The Sheep Mountain in Yukon that is the type locality of var. *kluanensis*, where the Alaska Highway skirts the base of the St. Elias Mountains at the south end of Kluane Lake, is now called Tachäl Dhäl (Southern Tutchone for "skin scraper mountain"). The varietal epithet *ovium* was replaced with *jepsonii* at the rank of species because of the strong potential for nomenclatural confusion with *P. ovina* J.M. Macoun, an unrelated species with an overlapping distribution (Ertter 2008).

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NEW AND NOTEWORTHY VASCULAR PLANT RECORDS FOR ALABAMA

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ABSTRACT

Ten non-native species (*Achyranthes japonica* var. *hachijoensis, Atocion armeria, Citrullus amarus, Cuscuta japonica, Cymbalaria muralis, Dioscorea alata, Grindelia ciliata, Odontonema cuspidatum, Paederia foetida,* and *Parentucellia viscosa*), four native species (*Clematis versicolor, Heteranthera multiflora, Pellaea glabella,* and *Quercus* x*beadleii*), five historic or uncommon species (*Asplenium ruta-muraria* var. *cryptolepis*, *Erigeron divaricatus, Philadelphus pubescens, Triglochin striata*, and *Wolffiella gladiata*), plus two varieties (*Paronychia erecta* var. *erecta* and *Vernonia angustifolia* var. *angustifolia*) of vascular plants are reported here as new to Alabama. A collection made in 2015 confirms the presence of *Erigeron divaricatus* in the state (previously known collections were prior to 1905). Similarly, *Asplenium ruta-muraria* var. *cryptolepis* was recently collected from multiple sites in two Alabama counties (last collected in 1877).

During the course of routine plant surveys extending to all portions of the state, 21 new/noteworthy records were collected. Each taxon is detailed in the write-up below. Species non-native (to Alabama) are designated with a dagger (†). Determination of nativity and state record status was ascertained by using the Alabama Plant Atlas (APA 2019), BONAP-Synthesis (Kartesz 2019), NatureServe (NatureServe 2019), SERNEC Data Portal (SERNEC 2019), the Flora of Southern and Mid-Atlantic States (Weakley 2015/pers. comm.), the Atlas of Georgia Plants (Zomlefer et al. 2019), and literature searches. Vouchered specimens are deposited in the Alabama Natural Heritage Section Heritage Herbarium (ALNHS), the Auburn University Herbarium (AUA), the University of West Alabama Herbarium (UWAL), and the Anniston Museum of Natural History Herbarium (AMAL). Exact plant locations are withheld due to the sensitive nature of the plant populations described and/or special permissions required for access to the sites.

ACHYRANTHES JAPONICA (Miq.) Nakai var**. HACHIJOENSIS** Honda (†) Japanese Chaff-flower (Amaranthaceae)

Vouchers. **Alabama.** Limestone Co.: Along edge of woods and roadside, at boat launch area leading to Elk River, 22 Jun 2015, *Barger and Taylor SP#1777* (ALNHS3256); low woods/floodplain along Elk River, N of Gipsy, 16 Aug 2015, *Spaulding DDS14,403* (UWAL34194). STATE RECORD.

Achyranthes japonica var. *hachijoensis* is the only extant *Achyranthes* species known from Alabama. Historic records of *Achyranthes aspera* L. were collected by Charles Mohr as waifs (collections determined by S. Ginzbarg and held at UNA) in 1892 from Mobile County, Ala, but are considered extirpated. Japanese Chaff-flower is considered highly invasive, commonly inhabiting moist floodplain soils, often with partial shading. Outside of the extensive populations that exist along the Ohio River (SERNEC 2019), only collections from three counties in both Georgia and Tennessee were known prior to these Limestone County, Ala, collections. Purported collections were made from Limestone County previously by Leon Bates, but searches to locate collections and attempts to contact the collector were not fruitful.

ASPLENIUM RUTA-MURARIA L. var**. CRYPTOLEPIS** (Fernald) Wherry American Wall-rue (Aspleniaceae)

Vouchers. **Alabama.** Jackson Co.: In cracks of large limestone boulders in hardwood forest, 1 Jul 2015, *Barger and Taylor HC#620*, (ALNHS3397). Lauderdale Co.: Along steep bluffs of calcareous rocks above Tennessee River, 30 Sep 2015, *Barger and Taylor SP#2042* (ALNHS3484). HISTORIC/UNCOMMON.

American Wall-rue has been considered a historical species for Alabama, with the only known collections (on the same herbarium sheet held at UNA) dating from 1877 by E.A. Smith and a second from 1908 by E.L. Lee. The confusing label for the mixed specimen reads, "Bibb (County) Pratt's Ferry; on rocks, sandstone; upper districts in mountains and northward to Kentucky; Gadsden, Etowah County; Sipsey Fork, Winston County." It is unclear which of the ferns, if any, represented on the sheet are from the locations stated. The reference to sandstone on the label is additionally perplexing, as the species usually inhabits calcareous/limestone rocks.

ATOCION ARMERIA (L.) Raf. (†) None-so-pretty (Caryophyllaceae)

Voucher. **Alabama.** Calhoun Co.: Through cracks in sidewalk, along Ala Hwy 9 in Piedmont, 14 May 2017, *Spaulding DDS14754* (ALNHS6146). STATE RECORD.

None-so-pretty is a commonly grown, self-seeding garden annual. More often encountered as a waif in the Northeast, this European native has been collected outside of the Blue Ridge only a few times in the southeastern USA. This waif from cracks in a sidewalk is the first collection known for Alabama.

CITRULLUS AMARUS Schrad. (†) Stockmelon (Cucurbitaceae)

Voucher. **USA. Alabama.** Montgomery Co.: Open pasture, observed for many years before determination, plants avoided by grazing livestock, full sun, 7 Nov 2014 and 28 Jul 2017, *Barger SP#1600* and *SP#3216* (ALNHS4795 and ALNHS5443). STATE RECORD.

This native of southern Africa has been reported from eleven counties in four western USA states (Kartesz 2019); however, this collection marks the first known collection east of the Mississippi River. The population was observed over the course of many years, with the perennial (from a thickened tap-rootstock) producing fruits that maintain a pale to yellowish mesocarp/endocarp when mature. The population spread throughout the pasture area during the course of observation.

CLEMATIS VERSICOLOR Small ex Rydb. Pale Leatherflower (Ranunculaceae)

Voucher. **Alabama.** Limestone Co.: Shady woods along high bluff of Elk River, rich hardwoods with mesic soils, 25 May 2012, *Barger SP#2903* (ALNHS4498). STATE RECORD.

Found in several MS and TN counties that border AL, *Clematis versicolor* was not known to occur in the state (APA 2019; Kartesz 2019). This specimen was collected on a high bluff of mesic hardwoods overlooking the Elk River rambling over shrubs/small trees of a fairly dense mid-story. Many stems were encountered; however, flowering specimens were few, likely due to the comparatively dense canopy. An incorrectly identified collection for the taxon had previously been reported from St. Clair County, Ala(Kartesz 2019).

CUSCUTA JAPONICA Choisy (†) Japanese Dodder (Convolvulaceae)

Vouchers. **Alabama.** Coosa, Tallapoosa, and Tuscaloosa Cos.: Roadside of highway, full sun; large, high-ramping masses parasitizing *Pueraria montana*, *Ligustrum sinense*, *Albizia julibrissin*, *Lonicera japonica*, and everything else it touched, 1 Jul 2017, *Barger and Barger SP#3223* and *SP#3323* (ALNHS5390 and ALNHS6043); roadside on Kudzu and Chinese Privet, off Mt. Moriah Road south of Vance, 29 Aug 2017, *Spaulding DDS14989* (ALNHS6042). STATE RECORD.

Listed as a Federal Noxious Weed, Japanese dodder is a highly aggressive parasitic plant that can quickly infest areas, and out-compete native flora. Unlike most other members of the genus, this Asian species often completely drapes over and decimates its host to the point of death.

CYMBALARIA MURALIS G. Gaertn., B.Mey. & Scherb. (†) Kenilworth Ivy (Plantaginaceae)

Voucher. **Alabama.** DeKalb Co.: Rock wall, stacked slabs of rock cemented with concrete; roadside near Ala Hwy 117 in Valley Head; Wills Valley of Cumberland Plateau, 14 Oct 2018, *Spaulding DDS15,785* (ALNHS6152). STATE RECORD.

Kenilworth Ivy is a European/Asian native that is commonly planted and has naturalized in many parts of the northern USA. This small, herbaceous but intricate-flowered plant is often used as a cover around rock walls.

DIOSCOREA ALATA L. (†) Winged Yam (Dioscoreaceae)

Voucher. **Alabama.** Baldwin Co.: E side of AlaHwy 98 and 4th street, climbing high into trees and over shrubberies, 30 May 2018, *Barger, Nation, and Long SP#4059* (ALNHS6009). STATE RECORD.

Discovered by Fred Nation, this vine produces abundant tubers, covers shrubs, and has the ability to climb high into the canopy. Though not documented from surrounding lots/areas, this location is dominated by the well-established vine. This Asian native was not known to occur in Alabama, but the noxious vine had been documented in neighboring Escambia, Jackson, and Santa Rosa counties, Fla (Kartesz 2019).

ERIGERON DIVARICATUS Michx. **(SYN = CONYZA RAMOSISSIMA** Cronquist) Dwarf Horseweed (Asteraceae)

Vouchers. **Alabama**. Madison Co.: St. John Paul II Catholic High School within the Huntsville city limits, sporadic on a small hillside lawn, NW side of property, 6 Aug 2017, *Finzel* s.n. (AMAL). Madison Co.: W side of Memorial Parkway, gravelly shaded parking lot, near edges of asphalt and lawn/concrete, 2 Jul 2018, *Barger SP#3982* (ALNHS6057). HISTORIC/UNCOMMON.

Erigeron divaricatus was known to occur in Alabama from three historical records (prior to 1905 held at UNC and AUA) and one subsequent collection from Limestone County, Ala, in 2015 (held at APSU). It generally occurs in disturbed clay soils and has now been documented in several other disturbed sites in Madison County along roadways. The combination of small stature, tiny flowers, and sporadic occurrences in disturbed habitats suggest that this plant has either been overlooked or is slowly becoming adventive in this area.

GRINDELIA CILIATA (Nutt.) Spreng. (†) Spanish Gold (Asteraceae)

Voucher. **Alabama.** Blount Co.: NE side of Ala Hwy 278; gravel shoulder, just E of Snead, three waif plants observed, samples taken from each, plants were not eradicated, 28 Sep 2016, *Barger and Taylor SP#2778* (ALNHS4500). STATE RECORD.

Native to the southern Great Plains, *Grindelia ciliata* may be becoming increasingly adventive, as indicated by the expanding collections across the upper/eastern plains region. However, outside of a waif collection in Calvert County, Maryland, from 1947 (Benedict *s.n.* US), the only collections from east of the Mississippi appear to be from two Michigan counties and a few scattered Illinois counties (Kartesz 2019). The nearest known collection to this northeastern Alabama collection was from approximately 560 km away in eastern Arkansas.

HETERANTHERA MULTIFLORA (Griseb.) C.N.Horn Purple-flowered Mud-plantain (Pontederiaceae)

Voucher. **Alabama.** Jackson Co.: In wet, depression in middle of access roadway; frequently mowed area, open field near tree, 1 Jul 2015, *Barger and Taylor HC#619* (ALNHS3197). STATE RECORD.

At present, the southeastern USA species of *Heteranthera* are under review, with potentially new species to be described. The Alabama populations with the many purple-flowers extending from the spathes match with material from mid-western populations of Kansas and Missouri (Horn, personal communication, 2019). It is possible, once they are reevaluated in the presence of new information, that a new name may eventually be assigned for these plants.

ODONTONEMA CUSPIDATUM (Nees) Kuntze (†) Firespike (Acanthaceae)

Voucher. **Alabama.** Mobile Co.: Along edge of wood-line, past the end of dead end Ingleside Drive; edge of USA nature trail property/firebreak, approx. 15 flowering plants, 18 Sep 2018, *Barger SP#4203* (ALNHS6103). STATE RECORD.

Introduced from Mexico and naturalized in several central Florida counties, this marks the first collection for Alabama (APA 2019; Kartesz 2019). Growing along the edge of a nature preserve/trails owned by the University of South Alabama, this species could have been discarded from an adjacent neighborhood; however, the population was definitely naturalized, with many flowering individuals present as well as immature plants.

PAEDERIA FOETIDA L. (†) Skunk Vine (Rubiaceae)

Voucher. **Alabama.** Baldwin Co.: Abundant high-climbing vine in remnant wet water oak/pine flatwoods; sandy soils S of sharp curve on Carver Lane, 18 Sep 2018, *Barger, Floyd, and Floyd SP#4196* (ALNHS6136). STATE RECORD.

Discovered by Carl Floyd while clearing private land, a sample was given to Fred Nation for examination/identification. This southeastern Asian species was not known to occur in Alabama, but the noxious vine had been documented in neighboring Escambia and Santa Rosa counties, Fla, as well (APA 2019; Kartesz 2019).

PARENTUCELLIA VISCOSA (L.) Caruel (†) Yellow Glandweed (Orobanchaceae)

Voucher. **USA. Alabama.** Baldwin Co.: Small population along wet roadside ditch of Rosco Road, at the intersection with Foley Beach Express, 6 May 2003, *Nation WBR1228* (ALNHS). STATE RECORD.

This European species appears to be most abundant in western USA (California, Oregon, and Washington) and has only been collected east of the Mississippi River once (Kartesz 2019). Later searches of the area have proven unproductive and the population is considered to have been a waif.

PARONYCHIA ERECTA (Chapm.) Shinners var**. ERECTA** Smooth Squareflower (Caryophyllaceae)

Vouchers. **Alabama.** Baldwin Co.: Sandy dune habitat, N of Ala Hwy 182, 27 Aug 2015, *Barger and Taylor SP#1966*, (ALNHS3514); Perdido Bay near Lillian; just above sandy shoreline, 15 Jun 2016, *Barger, Holt, and Taylor SP#2614* (ALNHS4258). UNRECORDED VARIETY.

Found scattered mainly in deep sandy soils along the northern gulf coastal regions from eastern La (one parish) to the central panhandle of Fla (Kartesz 2019), *Paronychia erecta* var. *erecta* has a glabrous, often glaucous stem; versus *P. erecta* (Chapm.) Shinners var. *corymbosa* (Small) Chaudhri,

which has a minutely gray, puberulent stem. It is doubtful that this is the first collection for the taxon from Alabama. However, determination to the varietal rank of specimens available all proved to be var. *corymbosa*. Closer examination of herbarium specimens will likely show this variety has been previously collected in Alabama.

PELLAEA GLABELLA Mett. ex Kuhn ssp. **GLABELLA** Smooth Cliff-brake (Pteridaceae)

Voucher. **Alabama.** Marshall Co.: High atop calcareous rock bluff along the Tennessee River, 21 May 2015, *Barger, Cressler, and Taylor SP#1697* (ALNHS3063). STATE RECORD.

Pellaea glabella subsp. *glabella* is one of the two more frequently encountered species of *Pellaea* in the eastern USA. The more abundant *Pellaea atropurpurea* (L.) Link is common throughout north/central Alabama. The closest known population of Smooth Cliff-brake to the Marshall County, Alabama site, however, was collected approximately 100 km away from Marion County, Tennessee. The Alabama population may also be the southernmost collection for the species, at approximately the same latitude as a collection from near Hot Springs, Arkansas.

PHILADELPHUS PUBESCENS Loisel. Hairy Mock-orange (Hydrangeaceae)

Voucher. **Alabama.** Limestone Co.: Shady woods along high bluff of Elk River, rich hardwoods with mesic soils, 25 May 2012, *Barger SP#2894* (ALNHS4471). HISTORIC/UNCOMMON.

Not previously known to occur in Alabama, a collection of *Philadelphus pubescens* was discovered while researching holdings for the species. The Ross Clark collection from 1966 is held at UNC (SERNEC 2019) and had been annotated (from the original determination of *Philadelphus hirsutus* Nutt.). This collection was not previously known to exist and had resulted in the species being omitted from various Alabama checklists (APA 2019; Kartesz 2019; Kral 2011). The author's collections represent the first known collections since the aforementioned and were discovered only a few miles northeast from that collection.

QUERCUS X BEADLEI Trel. ex Palmer Beadle's Oak (Fagaceae)

Voucher. **Alabama.** Lee Co.: Chewacla State Park, N side of Shell Toomer Parkway, 25 ft N of bike path, well-drained soils along margin of mixed hardwoods near West Pace Boulevard, 28 Sep 2018, *Schotz and Taylor CSP#565* (AUA78901). STATE RECORD.

This represents the first known collection of Beadle's Oak from Alabama. Collections are represented from 13 counties across 9 states ranging from east Texas to southern New Jersey (Kartesz 2019). The species is a putative hybrid of *Quercus alba* L. and *Quercus michauxii* Nutt., both of which have been documented in Lee County (APA 2019). Only one Beadle's oak was observed during the searches.

TRIGLOCHIN STRIATA Ruiz & Pavón Three-rib Arrow-grass (Juncaginaceae)

Voucher. **Alabama.** Mobile Co.: Underneath the N side of the Ala Hwy 163 bridge crossing Dog River, 17 Aug 2016, *Holt, Barger, and Taylor SP#2362* (ALNHS3993). HISTORIC/UNCOMMON.

Only three collections of this species are known from Alabama. Collected in 1878 (UNA), 1980 (USAM), and 1996 (AUA) from Baldwin and Mobile counties, it is unclear if this species is uncommon, unknown to most collectors, or simply overlooked. Thinly spread from eastern Louisiana Parishes along the Gulf/Atlantic coastal counties to Delaware (Kartesz 2019).

VERNONIA ANGUSTIFOLIA Michx. var. **ANGUSTIFOLIA** Tall Ironweed (Asteraceae)

Voucher. **Alabama**. Houston Co.: Just N of the Florida line, ca. 12 mi S Dothan, Ala, and ca. 6 mi NE of Graceville, Fla, N side of AME Road, frequent on dry sandy road bank with *Solidago brachyphylla, Quercus virginiana*, *Ilex vomitoria,* and *Chasmanthium laxum,* 16 Oct 2018, *Knapp and Highland 6117* (ALNHS6166). UNRECORDED VARIETY.

Treatments vary in recognition of infraspecific taxa for *Vernonia angustifolia*. The Flora of North America treatment recognizes no varieties (Strother 2006) whereas Weakley (2015) and Jones (1964) have recognized three varieties (var. *angustifolia*, var. *mohri*, and var. *scaberrima*). When infraspecific taxa are recognized, the only variety that has been attributed to the flora of Alabama is var. *mohrii* (Jones 1964; Kral et al. 2011; Weakley 2015). Previously var. *angustifolia* has not been attributed west of southcentral Ga (Jones 1964; Weakley 2015). This material was collected only a few meters north of Jackson County, Fla, and should be sought there.

WOLFFIELLA GLADIATA (Hegelm.) Hegelm. Sword Bogmat (Araceae)

Voucher. **USA. Alabama.** Madison Co.: Blackwell Swamp, frequent along the E side of swamp shoreline, 24 May 2018, *Barger and Long SP#3887* (ALNHS5980). HISTORIC/UNCOMMON.

Wolffiella gladiata is likely undercollected across its range due to its diminutive stature and aquatic habitat. While previously collected 28 times from 13 counties in Alabama, this collection marks the first collection north of the Fall Line for the state (Kartesz 2019). This location also is significant because it is the only collection for the entire Interior Low Plateau ecoregion (Kartesz 2019).

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FIRST REPORT OF *CALLICARPA DICHOTOMA* AND *CALLICARPA JAPONICA* (LAMIACEAE) SPONTANEOUS AND POTENTIALLY INVASIVE IN NEW YORK AND NEW JERSEY

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ABSTRACT

Spontaneous populations of *Callicarpa dichotoma* and *Callicarpa japonica* (Lamiaceae) are reported from New York and New Jersey for the first time. The populations are documented with herbarium specimens, photographs, and iNaturalist records. A dichotomous key to distinguish the native North American species and the commonly cultivated exotic species is provided.

At least three non-native species of *Callicarpa* are cultivated in the northeastern USA: the two reported here as adventive plus *Callicarpa bodinieri* H. Léveillé. The latter is rarely cultivated and can be distinguished by its large leaves with red abaxial leaf glands. It has not been found spontaneous in our region.

Callicarpa dichotoma (Lour.) K. Koch is a small shrub native to China, Vietnam, Korea, and Japan (Chen & Gilbert 1994). It is reported as naturalized in South Carolina (USDA, NRCS 2019), North Carolina (Radford & Ahles 1968), Kentucky (Campbell & Medley 2012), Tennessee (USDA, NRCS 2019), Virginia (Radford & Ahles 1968; Weakley 2015) and Delaware (USDA, NRCS 2019). According to Alan Weakley (2015), the species is beginning to spread more rapidly in the southeastern USA. The Delaware report of *Callicarpa dichotoma* can be confirmed with a specimen from Kent County (*Longbottom 15978*, NY). The Meehan Nursery in Pennsylvania was selling the species as early as 1879. It has been cultivated at the New York Botanical Garden since 1898.

Voucher specimens of *Callicarpa dichotoma*. New York. New York Co.: New York City, Manhattan, Central Park, Pond area, S of Gapstow Bridge, E side of Pond, between 61st and 62nd Street and between 5th and 6th Avenues, 40.766722, -73.973595, 26 Oct 2016, *Alvarez & Stout 201614* (NY);

Central Park, Dene Slope, 40.769302, -73.97117 (±20 m), 17 Aug 2018, *Gunderson 1* (NY). The Gapstow Bridge population consisted of one spontaneous individual and the Dene Slope population consisted of three spontaneous individuals.

Figure 1. *Callicarpa dichotoma* (A,B) and *Callicarpa japonica* (C,D), both spontaneous plants. A. Whole plant. B. Flowers with exserted stamens and small elliptic anthers. C. Whole plant. D. Flowers with exserted stamens and larger oblong anthers. (A,B. *Gunderson 1* (NY). C,D. *Young* <https://www.inaturalist.org/observations/20972366>).

Callicarpa japonica Thunb. is a shrub native to China, Japan and Korea (Chen & Gilbert 1994). Prior to this report it was only reported spontaneous in North Carolina (Weakley 2015; USDA, NRCS 2019). Spontaneous plants were observed at Tenafly Nature Center (40.923831, -73.941128, ±50 m) in Bergen Co., New Jersey, on 23 June 2018 (M. Young, iNaturalist observation: <https://www.inaturalist.org/observations/20972366>). The New York Botanical Garden has grown the species at least since 1936.

Voucher specimen of *Callicarpa japonica*. New York. Bronx Co.: New York City, Bronx, grounds of the New York Botanical Garden, South Arboretum, W side of the Bronx River, 40.857798N, -73.877060 (± 25 m, WGS 84), 18 May 2016, *Atha, Schuler, and Wang 15434* (NY). The Bronx County population consisted of one spontaneous individual. The Bergen County population consisted of five mature individuals.

Key to cultivated and spontaneous *Callicarpa* in the Northeast and Mid-Atlantic

1. Leaves ovate, densely pubescent below; peduncles shorter than the petioles (inflorescences sessile) ..... **Callicarpa americana**
1. Leaves elliptic, ± glabrous below; peduncles longer than the petioles (inflorescences stalked).
    2. Shrubs to 1.5 m tall; branchlets somewhat compressed, glabrous or with a few stellate hairs; leaves petiolate, 7–13 × 3.5–4 cm, the long caudate tip about 1/3 leaf length; anthers oblong, 1–2 mm long; cymes lax, each 3–4 cm across in fruit ..... **Callicarpa japonica**
    2. Shrubs to 1.3 m tall; branchlets terete or quadrangular, stellate pubescent; leaves subsessile, 2–6 (-10) × 1–3(-4) cm, the short caudate tip about 1/4 leaf length; anthers elliptic, ca 0.5 mm long; cymes dense, each 1–2 cm across in fruit ..... **Callicarpa dichotoma**

In addition to their displacement of native species, *Callicarpa* are congeners of a North American native and introgression of genetic material and erosion of genetic integrity of the native species should be a conservation concern. The sole *Callicarpa* species native to North America is *Callicarpa americana* L. This understory shrub usually occurs in moist or wet forests from Central Texas to Florida and north to southern Missouri, Tennessee, and Virginia (USDA, NRCS 2019).

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UNA NUEVA ESPECIE DE *JAEGERIA* (COMPOSITAE-MILLERIEAE) DEL CENTRO DE MÉXICO

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RESUMEN

Se describe como nueva y se ilustra a **Jaegeria rubustior** Rzed., **sp. nov.** con base en un ejemplar colectado en el sur del Estado de México, en las estribaciones meridionales del Eje Volcánico Transversal. Se le relaciona con *J. sterilis* McVaugh, procedente del estado de Jalisco, cuya ubicación en *Jaegeria* ya fue algo incómoda, pues no coincidía bien con el concepto generalmente aceptado del género hasta esa fecha. *J. robustior* se aleja aun bastante más de la anterior apreciación, pues es planta de mayor tamaño, sin liga con ambiente acuático y carente de alas basales de las brácteas involucrales. Sin embargo, se vincula con las demás especies conocidas de *Jaegeria* en las particulares características del aquenio, en los de la corola y del involucro, así como con *J. sterilis* y *J. pedunculata* Hook. & Arn. en la presencia de páleas tubulosas que encierran las partes basales de las flores del disco. Se postula que *J. sterilis* y *J. robustior,* especies al parecer estrechamente endémicas, corresponden a elementos relictos de un linaje antiguo que dio origen a otros componentes actuales de *Jaegeria.*

ABSTRACT

Jaegeria robustior Rzed., **sp. nov.**, is described as new and illustrated on the basis of a specimen collected in the south of the State of Mexico, on lower slopes of Transversal Volcanic Belt. It is related to *J. sterilis* McVaugh from the state of Jalisco, a species of somewhat uneasy location, because it did not coincide well with the accepted concept of the genus at that time. *Jaegeria robustior* is even much farther away from the former approach, being a larger plant with no links with aquatic habitat and lacking basal wings on the phyllaries. Nevertheless it is similar to the known species of *Jaegeria* in the peculiar characters of the achene and in those of the corolla and the involucre, as well as to *J. sterilis* and *J. pedunculata* Hook. & Arn. in the presence of tubular pales enclosing the base of disc flowers. It may be postulated that *J. sterilis* and *J. robustior,* both apparently narrowly endemic species, are relic elements of an old lineage that gave rise to other modern components of *Jaegeria.*

Recientemente llegaron a las manos del autor materiales de una planta de la familia Compositae que por sus características especiales no ha sido fácil de ubicar en alguna de las especies y géneros conocidos. Finalmente quedó definida como componente del género *Jaegeria,* a pesar del hecho de que, al menos a primera vista, se ve muy diferente de sus restantes especies conocidas.

JAEGERIA ROBUSTIOR Rzed., **sp. nov. TIPO**: **MÉXICO**. **Estado de México.** Mpio. Tonatico: Barranca del Río Los Amates, 18º47'26'' N, 99º42'10 W, laderas de rocas ígneas con vegetación de bosque tropical caducifolio, alt. 1613 m, herbácea perenne de 1 m de altura, flores blancas, 23 Sep 2011, *B. Bedolla, S. Lara C.,* y *S. Zamudio 115* (holotipo: IEB, isotipo por distribuirse). Figura 1.

Planta herbacea perennis ca. 1 m alta; caules erecti striati minute puberuli; folia opposita petiolis ad 3 cm longis, laminis ovatis vel ellipticis, principalibus ad 8 cm longis et 5.5 cm latis, apice acuminatis, base fere truncatis ad cuneatis, margine serrulatis ad fere integris, supra scabridis, subtus puberulis, triplinervatis membranaceis; inflorescentia sub formam panicularum terminalium parvarum conjuncte paniculam foliosam laxam ad 30 cm longam et 20 cm latam facientium, pedicellis ad 4 cm

longis; involucrum planum rotaceum phylariis 8 lanceolatis vel oblongis 2-2.5 mm longis, maturitate reflexis; receptaculum convexum paleis tubulosis ca. 1.5 mm longis, flororum partes basales omnino includentibus, rigidis persistentibus; flores radii 5 vel 6 steriles, ligulis oblanceolatis vel subflabellatis ca. 12 mm longis albis; flores disci ca. 35, corollis albidis vel cremeis, 2.5-3.5 mm longis, tubo ca. 0.7 mm longo abrupte dilatato, lobis 5 triangularibus; achaenia turbinata nigra glabra ca. 1 mm longa et lata fere epapposa.

Planta herbácea perenne de ca. 1 m de alto; tallos erectos, ramificados, rollizos, cafés claros, estriados, finamente pubérulos con pelos de menos de 0.1 mm de largo; hojas opuestas, peciolos hasta de 3 cm de largo, láminas ovadas o a veces las más pequeñas elípticas, las principales hasta de 8 cm de largo y 5.5 cm de ancho, las cercanas a la inflorescencia por lo general mucho más pequeñas, acuminadas en el ápice, casi truncadas a cuneadas en la base, serruladas a casi enteras en el margen, escábridas con pelos antrorsos y algo rasposas en el haz, pubérulas en el envés, triplinervadas, de textura membranácea; inflorescencia en forma de pequeñas panículas terminales de unas pocas o hasta unas 10 ramillas foliosas ubicadas en el extremo de las ramas principales de la planta, conformando en su conjunto una panícula foliosa laxa de hasta 30 cm de largo y 20 cm de diámetro y con alrededor de 50 cabezuelas, sus ejes pubérulos, pedicelos hasta de 4 cm de largo; involucro plano o casi plano, rotáceo, sus brácteas 8, lanceoladas a oblongas, de 2 a 2.5 mm de largo, todas de tamaño aproximadamente igual, agudas a redondeadas en el ápice, reflejas en plena madurez, verdes, pubérulas por fuera, glabras y uninervadas por dentro, de textura membranácea, sin alas basales, receptáculo provisto de páleas tubulosas de ca. 1.5 mm de largo y 1 mm de diámetro, puntiagudas en uno de los costados, glabras, que envuelven por completo las partes basales de las flores del disco, muy rígidas y persistentes por largo tiempo con los aquenios que rodean; flores del radio 5 o 6, estériles, carentes de estilo, lámina de la lígula anchamente oblanceolada a casi flabelada, de ca. 12 mm de largo y ca. 5 mm de ancho, cerca del ápice levemente emarginada, el tubo de ca. 3 mm de largo, blanca aunque con el secado tornándose amarilla, glabra en la mitad distal, pubérula en la proximal, su aquenio diminuto, negruzco; disco convexo, sus flores ca. 35, corolas blanquecinas o de color crema, de 2.5 a 3.5 mm de largo, mayormente pubérulas por fuera, el tubo más oscuro, de ca. 0.7 mm de largo, y 0.3 a 0.4 mm de diámetro, abruptamente dilatado en una garganta mucho más larga y de ca. 1 mm de diámetro, lóbulos 5, triangulares, de ca. 0.7 mm de largo, glabros, anteras cafés, ramas del estilo cafés a casi negras, de ca. 1 mm de largo, ensanchadas en la parte distal y luego puntiagudas en el ápice; aquenios de las flores del disco turbinados, negros, glabros, de ca. 1 mm de largo y de diámetro en el extremo distal, donde llevan una coronita muy inconspicua.

El taxón nuevo se conoce hasta ahora de una sola localidad, ubicada en las estribaciones inferiores del Eje Volcánico Transversal, pertenecientes a la cuenca del río Balsas. El lugar se encuentra muy próximo al límite con Guerrero, de manera que es probable la presencia de la especie también en ese estado. De cualquier manera se trata probablemente de un endemismo estrecho, ya que la región ya ha sido bastante intensamente explorada.

En varios rasgos de la inflorescencia, de las cabezuelas y de las flores, *Jaegeria robustior* está cercanamente relacionada con *J. sterilis* McVaugh, descrita y solo conocida de Jalisco. Las principales diferencias entre las dos especies se resumen en el Cuadro 1.

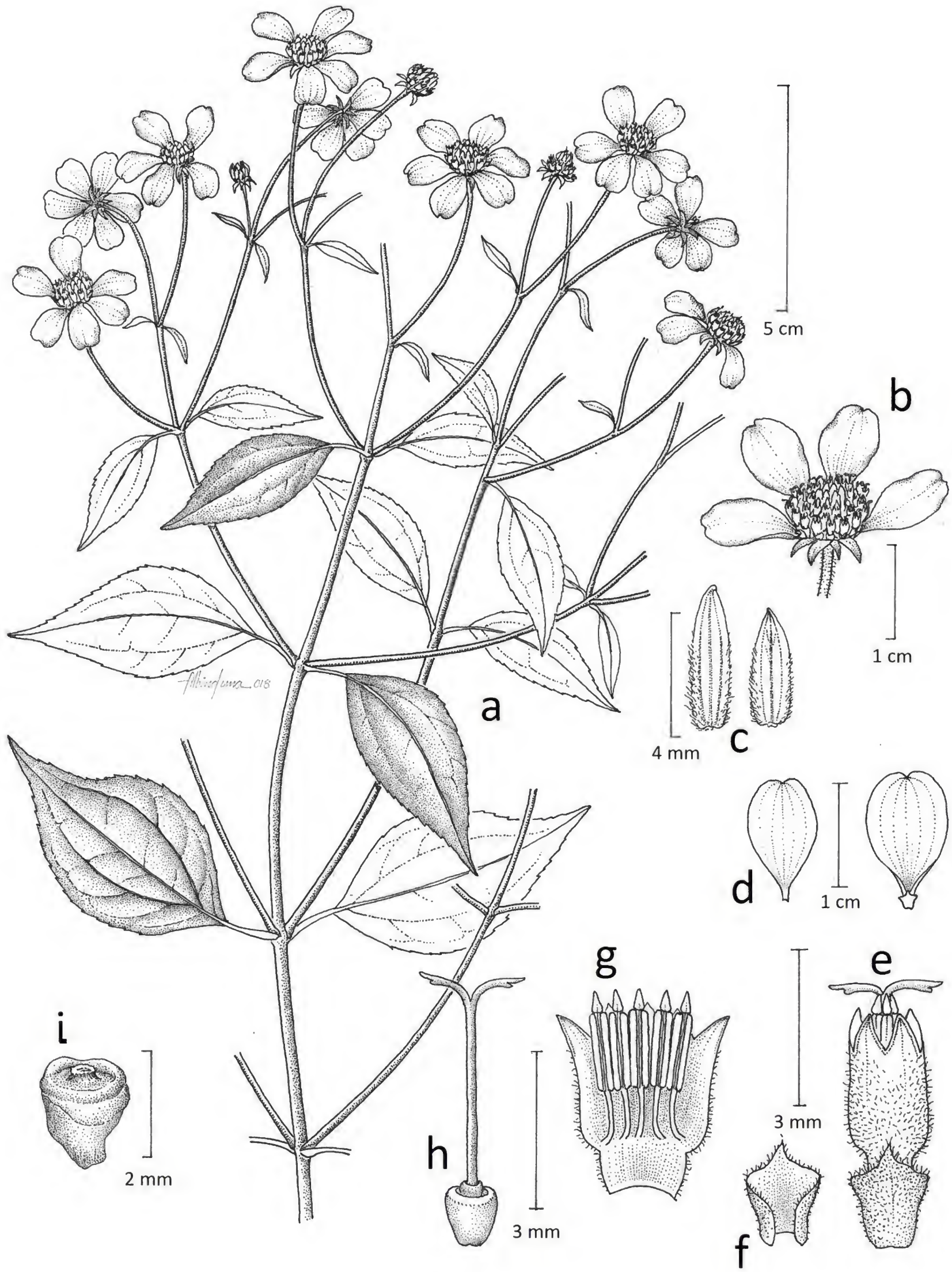

Figura 1. *Jageria robustior*. a. Rama con hojas e inflorescencia. b. Cabezuela con dos lígulas removidas. c. Brácteas involucrales. d. Flores liguladas. e. Flor del disco. f. Pálea envolvente. g. Corola de la flor del disco en corte longitudinal mostrando el androceo. h. Gineceo. i. Aquenio. Ilustrado por Albino Luna.

CARACTERES	*Jaegeria robustior*	*Jaegeria sterilis*
Porte	herbácea perenne de ca. 1 m de altura	herbácea anual de 10 a 20 cm de altura
Hojas	pecioladas, hasta de 8 cm de largo, pubescentes	sésiles, hasta de 3.5 cm de largo, casi glabras
Brácteas del involucro	sin alas basales	con alas basales de 2 a 2.5 mm de largo
Flores liguladas	anchamente oblanceoladas, de ca. 12 mm de largo, parcialmente pubescentes, sin estilo	elíptico-oblongas, de 4 a 6 mm de largo, glabras, con o sin estilo
Flores del disco		
corolas	de 2.5 a 3.5 mm de largo blanquecinas o de color crema	de 1.5 a 2.5 mm de largo, amarillas
anteras	cafés	verdosas
estilo, ramas	rectas, ensanchadas y puntiagudas en el ápice	encorvadas, lingüiformes
aquenios	turbinados, de ca. 1 mm de largo	cilíndricos, estrechados y encorvados en la base, de 1.3 a 1.7 mm de largo
Ambiente	bosque tropical caducifolio, alt. ca. 1600 m	prados húmedos de manantial, en medio de pinar, alt. 2200 m

Cuardo 1. Principales características diferenciales entre *Jaegeria robustior* y *J. sterilis*.

Con sus brácteas involucrales carentes de alas internas basales y su independencia del ambiente acuático o subacuático (ver Torres, 1968), cabe cuestionar seriamente la ubicación de la especie nueva en el género *Jaegeria.*

Sin embargo, se ha decidido situarla allí por las siguientes razones:

- gran similitud a *J. sterilis* en la esterilidad de sus flores del radio, en la forma de la inflorescencia, del involucro, de la corola, y sobre todo de las páleas, cuya estructura no tiene semejanza con la de otros representantes conocidos de la tribu Millerieae, a la que pertenece *Jaegeria,* de acuerdo con su clasificación actualizada (Panero y Funk 2002), aunque es algo análoga a las que se observan en las especies de *Sclerocarpus,* así como de *Aldama dentata* La Llave, de la tribu Heliantheae;
- su afinidad con otras especies de *Jaegeria* en la ausencia del vilano, en la forma y otros rasgos del aquenio, al igual que de la corola y de las brácteas involucrales.

En este contexto es interesante mencionar que McVaugh (1972, p. 421), en un comentario a la descripción de su *Jaegeria sterilis,* enfatizó también que esa especie no encaja bien en el concepto generalmente aceptado del género *Jaegeria*, pero se asemeja tanto a varias de sus especies, que no tuvo duda en ubicarla allí.

El mencionado autor hizo referencia al hecho de que ya en *Jaegeria pedunculata* Hook. & Arn. (aunque este no es el caso de las restantes especies conocidas del género) las páleas exteriores del receptáculo tienen forma envolvente similar a las de *J. sterilis* y de allí sugirió una posible secuencia evolutiva hacia el incremento de importancia de tales páleas. De ser correcta la hipótesis, la mencionada tendencia filogenética podría haberse continuado para desembocar en *J. robustior.*

En contra de tal planteamiento destaca la circunstancia de que tanto *Jaegeria sterilis* como *J. robustior* son aparentemente estrechos endemismos, mientras que las restantes especies de *Jaegeria* son plantas de mucho más amplia distribución geográfica y de hábitat acuático paulatinamente más definido.

De ser así, cabe especular postulando una secuencia evolutiva inversa, de acuerdo con la cual, *Jaegeria robustior* y *J. sterilis* podrían calificar como elementos relictos de un linaje antiguo del que habrían derivado los demás componentes actuales de *Jaegeria.*

El nombre de la especie nueva alude al hecho de que la generalidad de las especies conocidas del género son plantas de porte reducido (Torres 1968), mientras que *Jaegeria robustior* es un organismo más alto y voluminoso.

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Salywon, A.M. and W.C. Hodgson. 2019. *Agave simplex*, a new combination for Agavaceae. Phytoneuron 2019-219: 1–4. Published 25 April 2019. ISSN 2153 733X

AGAVE SIMPLEX, A NEW COMBINATION FOR AGAVACEAE

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ABSTRACT

Multiple lines of evidence indicate that *Agave deserti* subsp. *simplex* Gentry is more closely related to *A. mckelveyana* Gentry and *A. subsimplex* Trel. than to *Agave deserti* Engelm. In order to reflect these differences, *A. deserti* subsp. *simplex* warrants recognition at specific rank, thus the new combination **Agave simplex** (Gentry) Salywon & Hodgson, **comb. et stat. nov.**, is proposed. Distinguishing features and a distribution map are provided.

Gentry (1982: 376) called *Agave deserti* Engelm. "a large variable complex, the limits of which are hard to define." Initially this species was narrowly circumscribed as it was known only from a handful of collections, but the species concept grew to include a much wider range of populations as floristic and taxonomic treatments were published.

Agave deserti was first described from specimens collected near San Felipe, California. Based on the few specimens known to Engelmann and from communication with early collectors/explorers of the area, he described the range of the species as the "eastern base of the Southern California mountains and in the adjoining deserts" (Engelmann 1875: 310), in today's Imperial, Riverside and San Diego counties. Trelease (1911: 53) essentially followed Engelmann's delimitation of *A. deserti* noting its distribution as the "western border of the Colorado Desert in California." However, he also described *A. consociata* Trel. from the same type locality as *A. deserti* and described its distribution as extending into northern Baja California (Trelease 1911). *Agave consociata* is considered a synonym of typical *A. deserti* (Gentry 1982; Reveal & Hodgson 2002). Floristic works later expanded the concept of *A. deserti* to include disjunct agaves in the Whipple Mountains (Munz 1935) and later to the Granite, Old Dad, and Providence mountains, all in San Bernardino County, California (Munz 1965), and to western Arizona (Kearney & Peebles 1942; 1960). Gentry's (1972) taxonomic treatment expanded the distribution of *A. deserti* to include plants from northwestern Sonora, Mexico.

It is from within the broader concept of *Agave deserti* in Arizona that *A. mckelveyana* Gentry was described from the chaparral and juniper associations from between 3,000 and 6,000 ft in west-central Arizona. Gentry (1970: 227) stated "its nearest relatives appear to be *A. deserti* and *A. subsimplex* Trel. [from coastal central Sonora, Mexico and nearby islands]" and "I find no intergrading between them [*A. mckelveyana* and *A. deserti*] and believe the two groups to be biologically distinct species."

The description of *A. deserti* subsp. *simplex* Gentry from the Harquahala Mountains in west-central Arizona further recognized the distinctness of the eastern populations of *Agave deserti*. Gentry (1978: 24) noted that subsp. *simplex* is "a close relative of *A. mckelveyana,* which occupies higher montane elevations northeast of the *simplex* area."

Two independent lines of molecular genetic evidence support the close relationship of *Agave deserti* subsp. *simplex* to *A. mckelveyana* and *A. subsimplex* previously noted by Gentry. A population genetic study of the *A. deserti* complex (*A. deserti, A. cerulata* Trel., and *A. subsimplex*) by Navarro-Quezada et al. (2003), based on RAPD markers, supports a closer relationship of subsp. *simplex* to *A.*

subsimplex than to subsp. *deserti*. While phylogenetic studies of agaves in the USA and northwestern Mexico based on whole chloroplast sequence data (Salywon et al., unpubl. data) position subsp. *simplex* in a clade with *A. chrysantha* Peebles (from central Arizona), *A. mckelveyana*, and *A. subsimplex* and reveal that this clade is not closely related to subsp. *deserti*.

The morphological differences between *Agave deserti* subsp. *deserti* and subsp. *simplex* and *A. mckelveyana* are difficult to discern with most herbarium material. Additional fieldwork and a revision of the group is sorely needed to refine their species boundaries and construct better taxonomic keys. Nevertheless, given the data above from two separate molecular DNA studies, subsp. *simplex* warrants recognition at the species rank to more closely reflect its evolutionary position. In preparation for the publication of the Agavaceae assessment by the IUCN Cactus and Succulent Plant Specialist Group, we make the following combination.

Agave simplex (Gentry) A.M. Salywon & W.C. Hodgson, **comb. et stat. nov.** *Agave deserti* subsp. *simplex* Gentry, Occas. Pap. Calif. Acad. Sci. 130: 22. 1978. *Agave deserti* var. *simplex* (Gentry) W.C. Hodgson & Reveal, Novon 11: 413. 2001. **TYPE**: **Arizona**. Yuma Co. [now in La Paz Co.]: N slope of Harquahala Mountain, 12 mi W of Aguila, ca. 2500 ft, 12 Jun 1974, *H.S. Gentry 23404* (holotype: US-2826320, seen as image; isotypes: ARIZ!, DES-00010282!, MEXU).

Agave simplex is distinguished from *A. deserti* by its usually single or sparingly suckering habit (vs sparingly to prolifically suckering) and flower stalk with 8–17(–19) lateral branches in upper 1/3–2/5 of stalk (vs 8–22 in upper 1/5–1/3 of stalk). Additionally, its primary peduncle is relatively narrow, with a length to width ratio of 1.4–2.0 (vs. 1.2–1.6), and secondary and tertiary peduncles that are short (vs. primary peduncle wide, and secondary and tertiary peduncles much longer). *Agave simplex* flowers have filaments within the tube (vs. inserted at base of tepal lobes) and inner tepal lobes are generally narrower (1.5–5(–7) mm vs. 6–9 mm). *Agave simplex* occurs in southwestern Arizona (Mohave, Pinal, Pima, Yuma, La Paz, and Maricopa counties), southeastern California (San Bernardino County), southern Nevada (southern Clark County) and northwestern Sonora, Mexico, whereas *A. deserti* occurs in south-southcentral California (USA) and northcentral part of the state of Baja California, Mexico.

Differentiating *Agave simplex* from *A. mckelveyana* is more difficult. *Agave simplex* generally has a larger habit, longer leaves 25–40 cm long (vs. 20–35 mm), larger flower stalks (4–7.5 vs 2–3 m), and larger flowers 40–60 mm (vs. 30–40 mm), with larger tepal lobes, deeper and wider tube, and longer ovary.

Mapping the distribution of *Agave simplex, A. chrysantha, A. mckelveyana, A. subsimplex,* and *A. deserti* (subspp. *deserti* and *pringlei*) is also helpful to inferring relationships between these taxa (Fig. 1.). The map reveals a gap of at least ca. 150 km between *A. simplex* and *A. deserti*, with most of this gap being the rather inhospitable lower Colorado Desert, including the Colorado River, which could serve as a barrier to dispersal. In contrast, *A. simplex* is separated by less than 50 km from *A. mckelveyana* and *A. chrysantha*. Given the limited natural dispersal ability of most agaves, it is likely that related taxa would occur in closer versus distant geographical proximity. Thus, the molecular and geographic distributional data provide evidence that regional vicariance events shape the evolutionary history of these taxa more than long-distance dispersal.

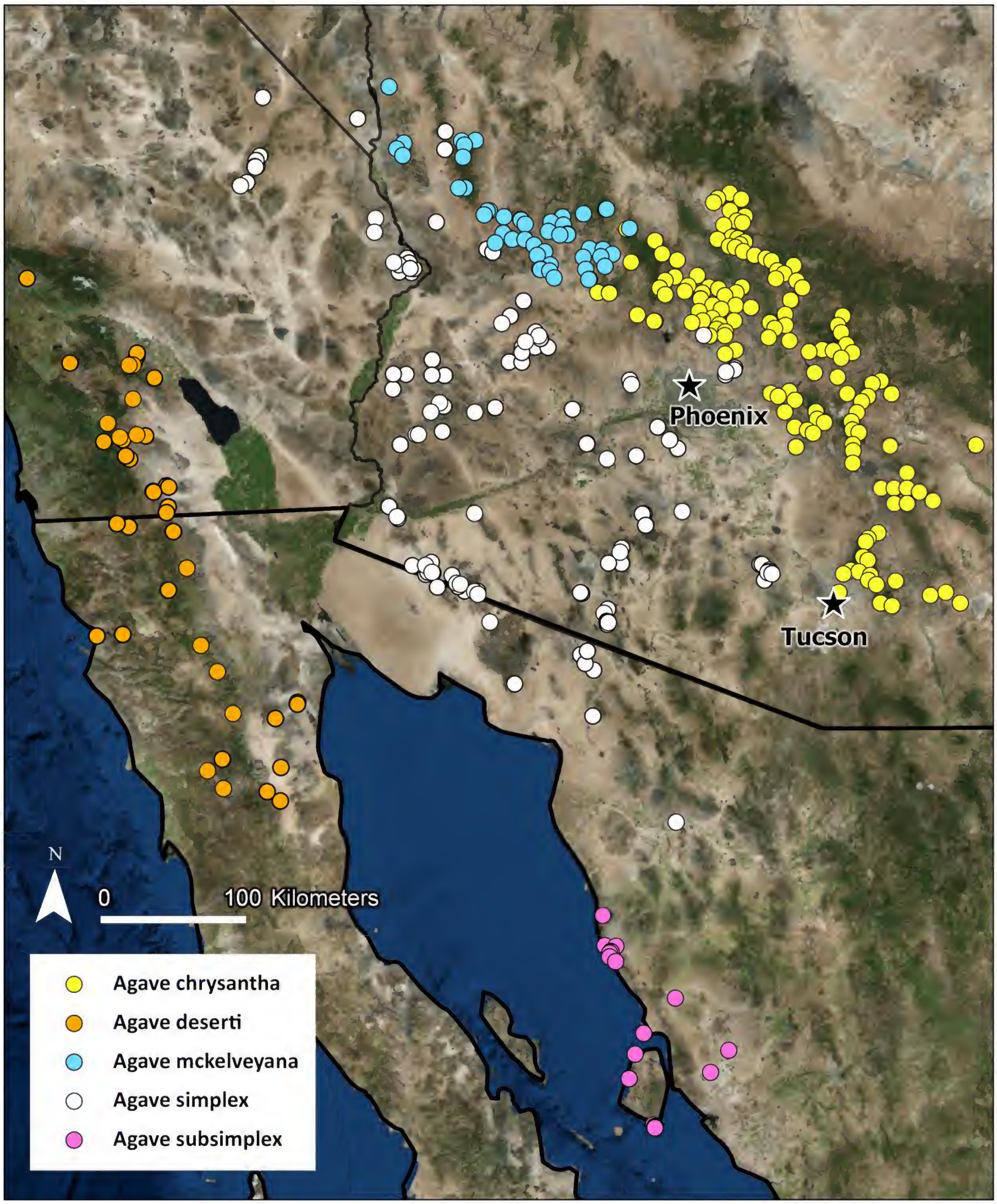

Figure 1. Distribution of *Agave simplex, A. chrysantha, A. mckelveyana, A. subsimplex,* and *A. deserti* (both subspp. *deserti* and *pringlei*) based on specimen data in SEINet (SEINET 2019). Base map source: Esri. "World Imagery" [basemap]. Scale Not Given. "World Imagery". March 13, 2019. <https://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer> Accessed 18 March 2019)

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SYMPHYOTRICHUM PRATENSE (ASTERACEAE) REDISCOVERED IN NORTH CAROLINA

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ABSTRACT

Recent field work has led to the rediscovery of *Symphyotrichum pratense* (Raf.) Nesom to the native North Carolina flora. A 2018 collection from Buncombe County is perhaps at or near the original locality, where it was collected over 200 years ago.

Symphyotrichum pratense (Raf.) Nesom is chiefly Coastal Plan in distribution, but its range extends into the Interior Low Plateaus, the Appalachian Plateau, and the Valley and Ridge of the central and eastern USA (Jones et al. 2008). The species occurs as far east as western Virginia, where it is known from Russell and Wise counties in dry, rocky woodlands and barrens over limestone and dolomite (Ludwig 1999; Virginia Botanical Associates 2019). Its presence in North Carolina is confirmed here.

Voucher. **North Carolina.** Buncombe Co.: Pisgah National Forest ca. 12 km (7.4 mi) NNE the city of Asheville, between Shope Creek Rd and Long Branch Rd, open glades in full sun, rare but patch dominant, usually over seepage on rock, 35.6480° -82.4289, elev. 3700 ft, 20 Sep 2018, *Knapp & Kelly 6100* (NCU); 24 Sep 2018, *Knapp et al. 6111* (NCU).

Before the collection reported here, there was a single, undated collection (*Gibbs s.n.*, NY) from "Buncombe, N. Car", in the Blue Ridge Physiographic Province of North Carolina. In 1816 Thomas Nuttall traveled from Tennessee to Asheville, Morganton, and Rutherfordton, North Carolina (Graustein 1967). Two years later (Nuttall 1818) he described *Aster montanus* Nutt. and cited the Gibbs collection referenced above. The original discovery of *Symphyotrichum pratense* in North Carolina was widely overlooked and the species was not included in North Carolina floras (Radford et al. 1968; Weakley 2015) until Jones et al. (2008) noted its historical presence. Thus, the 2018 collection marks the first documentation of this species from North Carolina and the Blue Ridge Physiographic Province in over 200 years.

The 2018 collection is from the same county as the historical Gibbs collection. It is even possible that this is the same location as the Gibbs collection, but access to this area is difficult and there are no nearby roads.

The range of habitats for *Symphyotrichum pratense* includes prairies, oak woodlands, pine-oak scrub, fields, and roadsides, often with a calcareous influence (Brouillet et al. 2006; Jones et al. 2008). The habitat in North Carolina is best described as Low Elevation Basic Glades – Montane Subtype (Schafale 2012). These glades are characterized as having a sparse tree and shrub canopy with patches of bare rock, mats of the spikemoss *Bryodesma rupestre* and various basophilic indicator plants such

as *Myriopteris lanosa* and *Hylotelephium telephioides*. Low Elevation Basic Glades generally have a southerly or westerly aspect and can be steep or gently sloping.

Symphyotrichum pratense is rare on these glades but forms patches of over 100 plants in limited areas of seepage over bedrock. These glades are considered a globally rare natural community, ranked as G2 (Schafale 2012). Nine species tracked by the North Carolina Natural Heritage Program (Robinson 2018) also are found on or immediately surrounding these glades, and include *Allium allegheniense*, *Arabis pycnocarpa* var. *adpressipilis, Draba ramosissima*, *Primula meadia, Packera millefolium*, *Phlox subulata*, and *Rudbeckia triloba* var. *beadlei*. *Carex roanensis* and *Silene ovata* also are found in the open woodland surrounding these glades. If added to the North Carolina tracking list, *Symphyotrichum pratense* will become the 13th species of the genus tracked in the state.

Interestingly, these Buncombe County glades have been surveyed repeatedly yet the *Symphyotrichum* has not been documented (NCNHP Biotics Database 1985, 2007, 2008). When not in flower, *S. pratense* is easy to overlook as the leaves blend in with the abundant vegetation at the site, but when in flower, the deep magenta corollas, and large size of the plants are nearly impossible to overlook (Fig. 1, Fig. 2, & Fig. 3).

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Figures 1 (top) and 2 (bottom). *Symphyotrichum pratense* at the Buncombe County locality.

Figure 3. *Symphyotrichum pratense* at the Buncombe County locality.

Lomer, F. 2019. *Erythranthe scouleri* (Phrymaceae) native in the Fraser River Delta tidelands, British Columbia. Phytoneuron 2019-21: 1–8. Published 25 April 2019. ISSN 2153 733X

ERYTHRANTHE SCOULERI (PHRYMACEAE) NATIVE IN THE FRASER RIVER DELTA TIDELANDS, BRITISH COLUMBIA

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ABSTRACT

Erythranthe scouleri (Hook.) Nesom is restricted to estuaries and tidelands on the Columbia River (Oregon and probably Washington) and Fraser River (British Columbia). Its occurrence in the Fraser River delta of British Columbia is documented by collections reported here. The morphology of the species is shown in photos of herbarium specimens and plants in nature.

Erythranthe scouleri (Hook.) Nesom is a little-known monkeyflower that in the past was lost in the *Mimulus guttatus* DC. complex. It was originally named *M. scouleri* from material collected by John Scouler on the Columbia River in Oregon and later treated as a distinct species (Howell 1903; Pennell 1951). In Hitchcock et al. (1959) it was listed in synonymy of *Mimulus guttatus* as *M. guttatus* subsp. *scouleri* (Hook.) Penn. Nesom treated it as a distinct species in 2012 and it is now included as such in the Flora of the Pacific Northwest Second Edition (Legler 2018).

At the time of Nesom's publication in 2012, *Erythranthe scouleri* was known only from the type specimens at K and NY (Columbia River, Oregon) and a few other collections.

ERYTHRANTHE SCOULERI (Hook.) Nesom, Phytoneuron 2012-40: 44. 2012. *Mimulus scouleri* W.J. Hook., Fl. Bor.-Amer. 2: 100. 1838. *Mimulus guttatus* subsp. *scouleri* (Hook.) Penn., Proc. Acad. Nat. Sci. Philadelphia 99: 166. 1947. **TYPE**: **USA**. **Oregon**. [probably Clatsop Co.]: Columbia River, no date, *Dr. Scouler s.n.* (holotype: K image!; isotype: NY image!).

Oregon. [Clatsop Co.:] S shore of Columbia River, above Astoria, 1883, *Meehan 15739* (MO); John Day, 20 Aug 1902, *Sheldon 10181* (UC); John Day, near Tongue Point, 20 Aug 1902, *Sheldon 11136* (MO). The two Sheldon collections apparently were made from the John Day River near Astoria in Clatsop County, not the town of John Day in Grant County, nor from the other John Day River, which enters the Columbia at the eastern border of Sherman County. See Nesom (2013) for a record from Columbia County, Oregon.

Plants of *Erythranthe scouleri* are perennials (proximal nodes often adventitiously rooting and producing slender rhizomes/stolons) up to more than a meter tall and often loosely sprawling over other vegetation, with yellow corollas to 5 cm long. They are recognized especially by the narrowly lanceolate to elliptic mid-stem leaves, unlike the rounded leaves of *E. guttata* or any of the related species in the complex, and long petioles on the lower stem. The proximal leaves often are disintegrated and muddy at flowering time and the distal leaves become rounded near the inflorescence, as in *E. guttata*. Nesom (2012) described *E. scouleri* as glabrous throughout, based on limited material, but the peduncles and pedicels, bracts, and calyces of plants from the Fraser River area are sparsely glandular with fine, clear, flattened, septate hairs mostly topped with a small, golden brown, globular gland.

Several British Columbia botanists were familiar with *Erythranthe scouleri* on the Fraser River tidelands but failed to recognize it as distinct from *E. guttata*. It now can be understood, however, that *E. scouleri* is a Pacific coast endemic, restricted to estuaries and tidelands on the Columbia and Fraser Rivers, including several sites in the Fraser River delta in British Columbia. A search for this species was conducted in an area of the Squamish River estuary, 55 kilometers north of the Fraser River on 14

July 2018, but no *Erythranthe* species were found. *Erythranthe* was reported from the Courtenay River estuary on Vancouver Island in similar tideland mud habitats, but these plants proved to be typical *E. guttata*. Although *E. guttata* and *E. scouleri* can share the same estuary habitat, they have not yet been observed in close proximity.

Documentation for British Columbia collections is below. Vouchers are deposited in the University of British Columbia herbarium (UBC), with duplicates to CAN, DAO, TEX, V, and WTU.

Canada. **British Columbia**. Ladner, Delta (a suburb of Vancouver), tidal marsh, 10 Jul 1979, *Bradfield & Porter 64* (UBC); Metro Vancouver, Delta, island in Fraser River at W end of Tilbury Slough, 700 m NE of Deas Island, tidal marsh, 29 Aug 2014, *Lomer 8942* (UBC); Metro Vancouver, Delta, Deas Island, SW shore, opposite Captain's Cove Marina, tidal marsh, with *Equisetum fluviatile*, *Oenanthe sarmentosa*, *Lycopus europaeus*, *Agrostis gigantea*, *Trifolium wormskioldii*, *Lythrum salicaria*, *Symphyotrichum subspicatum*, and *Carex lyngbyei*, 4 Jul 2018, *Lomer 11224* (UBC); New Westminster, Queensborough, Annacis Channel, Fraser River shore, 50 m E of South Dyke Road and Suzuki Street, tidal marsh strip, with *Equisetum fluviatile*, *Phalaris arundinacea*, *Oenanthe sarmentosa*, *Lycopus europaeus*, *Lythrum salicaria*, *Lotus corniculatus*, *Iris pseudacorus*, *Rumex occidentalis*, *Symphyotrichum subspicatum*, *Carex cusickii*, *Impatiens capensis*, *Juncus oxymeris*, and *Platanthera dilatata*, 6 Jul 2018, *Lomer 11226* (UBC); New Westminster, Queensborough, 270 m NE of Annacis Channel bridge over Fraser River, 20 m S of South Dyke Road, tidal marsh strip, *Equisetum fluviatile*, *Carex lyngbyei* margin, with *Phalaris arundinacea*, *Myosotis scirpioides*, *Lycopus europaeus*, *Lythrum salicaria*, *Lotus corniculatus*, *Iris pseudacorus*, *Bidens cernua*, *Leersia oryzoides*, and *Symphyotrichum subspicatum*, 6 Jul 2018, *Lomer 11227* (UBC); Metro Vancouver, Delta, Annacis Island, NW side, 645 m due SW of Highway 91 bridge, Fraser River tidal marsh, with *Equisetum fluviatile*, *Carex lyngbyei*, *Lycopus europaeus*, *Lythrum salicaria* and *Juncus oxymeris*, 1 Aug 2018, *Lomer 11297* (UBC); Metro Vancouver, Delta, Annacis Island, western end, 65 m N of western tip, Fraser River tidal shore, in thick vegetation under hydroelectric lines, with invasive *Lythrum salicaria*, *Lycopus europaeus*, *Iris pseudacorus*, *Sidalcea hendersonii*, *Epilobium ciliatum* subsp. *watsonii*, *Phalaris arundinacea*, *Trifolium wormskioldii*, and *Caltha palustris*, 1 Aug 2018, *Lomer 11303* (UBC); Metro Vancouver, Burnaby, North Arm of Fraser River, 90 m E of foot of Boundary Road, upper tidal shore, poking up through flattened *Carex* mat, scattered plants in limited area below wide path with fence along warehouses, below cement chunks and rock dyke, muddy substrate, in thick vegetation with *Leersia oryzoides*, *Lythrum salicaria*, *Phalaris arundinacea*, *Agrostis stolonifera*, *Impatiens capensis*, *Carex lyngbyei*, and *Bidens cernua*, 29 Aug 2018, *Lomer 11428* (UBC).

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Figure 1. *Erythranthe scouleri*, *Bradfield & Porter 64* (UBC).

Figure 2. *Erythranthe scouleri*, *Lomer 8942* (UBC).

Figure 3. *Erythranthe scouleri*, *Lomer 11224* (UBC).

Figure 4. *Erythranthe scouleri*, *Lomer 11226* (UBC).

Figure 5. *Erythranthe scouleri*, *Lomer 11227* (UBC).

Figure 6. *Erythranthe scouleri* on the Fraser River in New Westminster, British Columbia. Photos by Ryan Batten.

Semple, J.C. and F. Jabbour. 2019. Type specimens of *Inula (Pityopsis) graminifolia* (Asteraceae: Astereae). Phytoneuron 2019-22. 1-9. Published 25 April 2019. ISSN 2153 733X

TYPE SPECIMENS OF *INULA (PITYOPSIS) GRAMINIFOLIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Recent proposed changes to the nomenclature of the goldenaster genus *Pityopsis* disagreed significantly on the application of the name *Inula graminifolia*, the basionym of *Pityopsis graminifolia*. In order to clarify the problem, the three known collections of *Inula graminifolia* in the Herbarium of the Muséum national d'Histoire naturelle, Paris (P) collected by André Michaux were examined. The holotype collection has small heads with many stipitate glands on the distal portion of the phyllaries and obvious long hairs on the peduncles. This is also the case for the isotype collection. A third collection by Michaux is mixed with a shoot with larger heads and shoots with smaller heads and all with phyllaries with few or no stipitate glands. Thus, the third specimen is not part of the same taxon as the holotype and isotype.

The *Pityopsis graminifolia* (Michx.) Nutt. complex includes goldenasters native to the southeastern USA, southern Mexico, Guatemala, Belize, western Honduras, and the Bahamas. The complex includes either a single species with multiple varieties (Semple & Bowers 1985; Semple 2006) or the complex might be divided into multiple species with more narrowly defined morphological and ecological limits. Semple and Bowers (1985) presented a revision of the genus *Pityopsis* Nutt. recognizing seven species. Four species were placed in *P.* sect. *Pityopsis* and all are narrowly to very narrowly distributed species. *Pityopsis pinifolia* (Elliott) Nutt. is a rare species found along the eastern edge Piedmont along the "fall line" counties of North Carolina, South Carolina, and Georgia, (and Mississippi, Nesom 2019). *Pityopsis falcata* (Pursh) Nutt. is native to the Atlantic Coastal plain from Cape Cod, Massachusetts to southern New Jersey. *Pityopsis flexuosa* (Nash) Small is native to a few counties around Tallahassee, Florida. *Pityopsis ruthii* (Small) Small is confined to a small area in southeastern Tennessee along short sections of the Hiwassee and Ocoee Rivers (Moore et al. 2016). Three additional species were included in *P.* sect. *Graminifoliae* (Small) Semple. *Pityopsis oligantha* (Chapm. ex Torr. & A. Gray) Small has big glandular heads and occurs in the Florida Pandle and adjacent counties in Alabama and Georgia. *Pityopsis aspera* (A. Gray) ex Small has glandular peduncles and includes two varieties: var. *aspera* is confined to a small area in southern Georgia and adjacent northern Florida; var. *adenolepis* (Fernald) Semple & F.D. Bowers occurs from northeastern Virginia to northern Florida and west to southern Mississippi. Lastly, there is the more widely distributed species *P. graminifolia* in the broad sense, occurring from Delaware to southern Ohio and south to southern Florida, and west through the southern states to eastern Texas and disjunct in Latin America as noted above; most forms of the species have long narrow lower stem and rosette leaves and all have peduncles with long white cobwebby hairs. Five varieties were recognized within *P. graminifolia* by Semple and Bowers (1985, and followed in Semple 2006). Diploid var. *graminifolia* was defined on the basis of having smaller heads with inner phyllaries that

are obviously stipitate glandular (Fig. 1); such plants occur from southern North Carolina to northern Florida and west to Mississippi on the outer coastal plain. Diploid var. *tenuifolia* (Torr.) Semple & F.D. Bowers has small heads with inner phyllaries that are not strongly glandular; *Chrysopsis microcephala* Small and combinations on that name were treated as synonyms; var. *tenuifolia* in this sense occurs from North Carolina to southern Florida and west to east and south Texas and extending north into Arkansas and extreme eastern Oklahoma. Diploid var. *aequilifola* F.D. Bowers & Semple has smaller heads and stiff densely-arranged ovate-lanceolate stem leaves and occurs in Peninsula Florida. Tetraploid and rarely hexaploid var. *latifolia* (Fernald) Semple and F.D. Bowers has mid-sized heads with phyllaries that are not glandular (or with a few obscure glands); the stem leaves are narrowly lanceolate; the range occupies the entire area described for the species. Hexaploid var. *tracyi* (Small) Semple has large heads without obvious glands and is confined to the Florida Panhandle. Ploidy level data was presented and summarized in Semple and Bowers (1987) with additional counts reported by (Semple & Cook 2004; Semple et al. 2015, 2019 in press).

Recently, Bridges and Orzell (2018), focusing on the Peninsula Florida taxa proposed breaking up *P. graminifolia* in the broad sense into five species. *Pityopsis graminifolia* was noted to have small heads with glandular phyllaries which follows the application of the name by Semple and Bowers (1985). *Pityopsis aequilifolia* (F.D. Bowers & Semple) E.L. Bridges & Orzell occurs "exclusively on xeric sands, in both Florida scrub and fire-prone sandhills within central Florida" (Bridges & Orzell 2018). *Pityopsis microcephala* Small was noted to have very narrow leaves and that further study supporting it as a separate species distinct from *P. graminifolia* was needed across the range of the two taxa. *Pityopsis tracyi* (Small) Small was noted to have large involucres 12-14 mm high and to have robust lower stem and rosette leaves and was confined to "somewhat poorly to poorly drained pine savannas and seasonally wet grasslands with a historical high fire return interval" in Peninsula Florida. *Pityopsis latifolia* (Fernald) Bridges & Orzell was considered to have involucres 8-12 mm high and to have few soft narrow stem leaves and be restricted to southern Florida. Bridges and Orzell (2018) noted their uncertainty about how to deal with plants included in *P. graminifolia* var. *latifolia* by Semple and Bowers (1985) outside Peninsula Florida and taxonomic problems with applying other names listed in synonymy in Semple and Bowers (1985) to possibly separate races, e.g., names based on and *Erigeron nervosus* Willd., synonym *Pityopsis nervosa* (Willd.) Dress and *Chrysopsis correllii* Fernald.

Even more recently Nesom (2019) proposed an alternative approach to the broadly delimited *Pityopsis graminifolia* with very different results from Bridges and Orzell (2018) in how some names were applied. Nesom (2019) recognized 12 species of *Pityopsis* with the delimitations of *P. aspera*, *P. falcata*, *P. flexuosa*, *P. oligantha*, *P. pinifolia* and *P. ruthii* being in agreement with Semple and Bowers (1985) and Semple (2006). The dot distribution map for *P. pinifolia* shows many more collections and one from Alabama, which were not known by Semple and Bowers (1985) because the location was uncertain and was the neotype for the species selected by Semple and Bowers (1985). Nesom (2019) split *S. graminifolia* sensu lato into 6 separate species that do not correspond to varieties in Semple and Bowers (1985) and Semple (2006). Most significantly, the name *P. graminifolia* is applied to what was *P. graminifolia* var. *latifolia* in Semple and Bowers (1985) and Semple (2006) and *P. tracyi* was expanded to include diploid and tetraploid plants from Peninsula Florida as well as the large headed hexaploids included in *P. graminifolia* var. *tracyi* by Semple and Bowers (1985) and Semple (2006). Nesom (2019) delimited *S. aequilifolia* the same way that Semple and Bowers (1985) and Semple (2006) delimited *S. graminifolia* var. *aequilifolia* but at species rank. Nesom (2019) applied the name *P. microcephala* to small headed plants with densely stipitate glandular phyllaries and mapped a range that is similar to that of *P. graminifolia* var. *graminifolia* in Semple and Bowers (1985). Plants that were included in var. *microcephala* in Semple and Bowers (1985) and Semple (2006) were treated as *P. tenuifolia* (Torr.) Nesom occurring west of the Mississippi River, and into other taxa east of the Mississippi.

Nesom (2019), working from online digital images, considered that P00742815 (Fig. 2) was the holotype of *Inula graminifolia* and that P00742818 (Fig. 3) included one isotype shoot of *P. latifolia* and two shoots of *P. microcephala*. These conclusions needed further investigation and the results are presented below.

In 1984, the first author visited the Muséum national d'Histoire naturelle in Paris and examined a Michaux collection (Fig. 1) included in the P-MICH historical collection (Thiers, continuously updated). This was a short visit and only specimens on a list sent earlier by mail were provided for examination. The holotype of *Inula graminifolia* was one of the specimens included on the list. Stipitate glands were observed on the small heads of the single shoot on the specimen (Fig. 4), which bore a TYPE label at the time and an annotation by William T. Gillis dated 1 juin 1976 and noting that the specimen was the type of *Inula graminifolia* Michx. The first author annotated the specimen as the holotype of *Inula graminifolia* and took several black and white photographs during the 1984 visit. This was the only Michaux collection of *Inula graminifolia* examined in 1984 and is the only one of the three Michaux collections examined in preparing this publication that includes a handwritten label indicating the classification of the specimen at the time. The second author compared the writing with known hand script of André Michaux and concluded that the label was likely written by Michaux himself. Thus, this collection is the only real choice for holotype of *Inula graminifolia*, the basionym of *Pityopsis graminifolia*. Only plants with small heads and stipitate glands on the phyllaries can be included in *P. graminifolia* var. *graminifolia*, as was done by Semple and Bowers (1985) and Semple (2006), or in a narrowly defined *P. graminifolia* as done by Bridges and Orzell (2018). Involucres on the holotype averaged about 5.6 mm high.

The other two Michaux collections (P00742818 and P00742815) were not seen by the first author in 1984 and were examined at his request by the second author in 2019. Both collections have a printed ISOTYPE label on the sheets. The three shoots on P00742818 have small heads (involucres averaging 6.1 mm tall) and phyllaries with glands (Figs. 2 and 5). Thus, P00742818 is similar to the holotype and is treated here as an isotype of *Inula graminifolia*. The two shoots on P00742815 differ in head size (taller left shoot with involucres averaging 9.1 mm high; right shoot with involucres averaging 8.8 mm); both shoots have phyllaries with few or no glands (Figs. 3 and 6). Therefore, P00742815 is not the same taxon as the holotype of *Inula graminifolia* and should not be considered as an isotype. Shoot "a-b" and shoot "d" are all part of the Michaux collection, acquired at one point by the E. Drake herbarium. The material was included in P in a second step.

A much larger study is needed to resolve questions on whether splitting up *Pityopsis graminifolia* into more narrowly defined separate species and how many species should be recognized. If additional research determines that *P. latifolia* should be limited to plants in Florida, then *Pityopsis nervosa* (Willd.) Dress [Baileya 19: 166. 1975.] based on *Erigeron nervosus* Willd. [Sp. Pl., 3: 1953. 1803.] is the oldest species epithet to apply to the much more widely distributed species level taxon occurring in much of the southeastern USA, southern Mexico, Guatemala, and Belize. The Bahamian populations could belong to *P. latifolia* or *P. nervosa* depending upon study results. Further work is needed to determine whether it is appropriate to split these small headed non-glandular *P. microcephala* into an eastern taxon under that name and a western *P. tenuifolia*. A multivariate study of the kind being done on multiple groups of *Solidago* recently might provide a solution to these problems (e.g., Semple et al. 2017; Semple et al. 2018). Cutting edge DNA based research may also provide solutions, if polygenomic sampling is utilized on sufficient numbers of specimens (see Wadl et al. 2011). Single gene or internal transcribed spacer sequencing will probably not be sufficient (Brouillet et al. 2009). The first author has split *Solidago* into many more species in recent years (Semple 2019) than were recognized in 2006 and would likely conclude that splitting a broadly defined *P. graminifolia* into 5-6 or more species now is an appropriate solution at this time pending results of new studies. Selecting the correct names to apply will necessitate doing more than

looking at online digital images of type collections because critical indument details are not clearly visible even on the higher resolution images now available. Counting the numbers of hairs and glands on phyllaries will be tedious but may be necessary after assembling a large sample of *Pityopsis* herbarium collections from the entire range of the species and including all races. Using a dissecting scope at 40-70× magnification is still a necessity in modern systematic botany.

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Figure 1. Holotype of *Inula* (*Pityopsis*) *graminifolia*, *Michaux s.n.* (P-MICH). No bar code.

Figure 2. Isotype of *Inula* (*Pityopsis*) *graminifolia*, *Michaux s.n.* (P00742818). <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00742818>

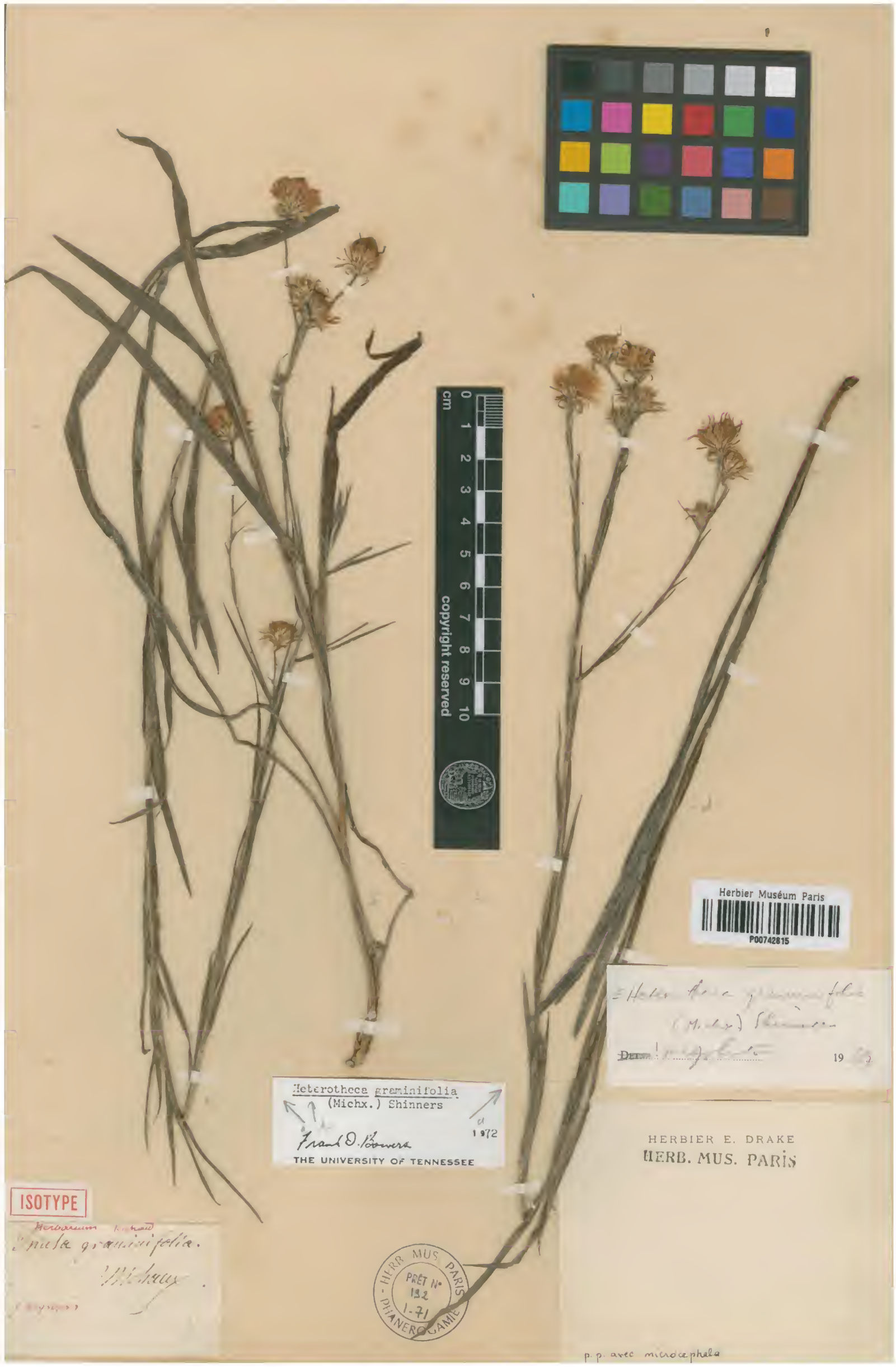
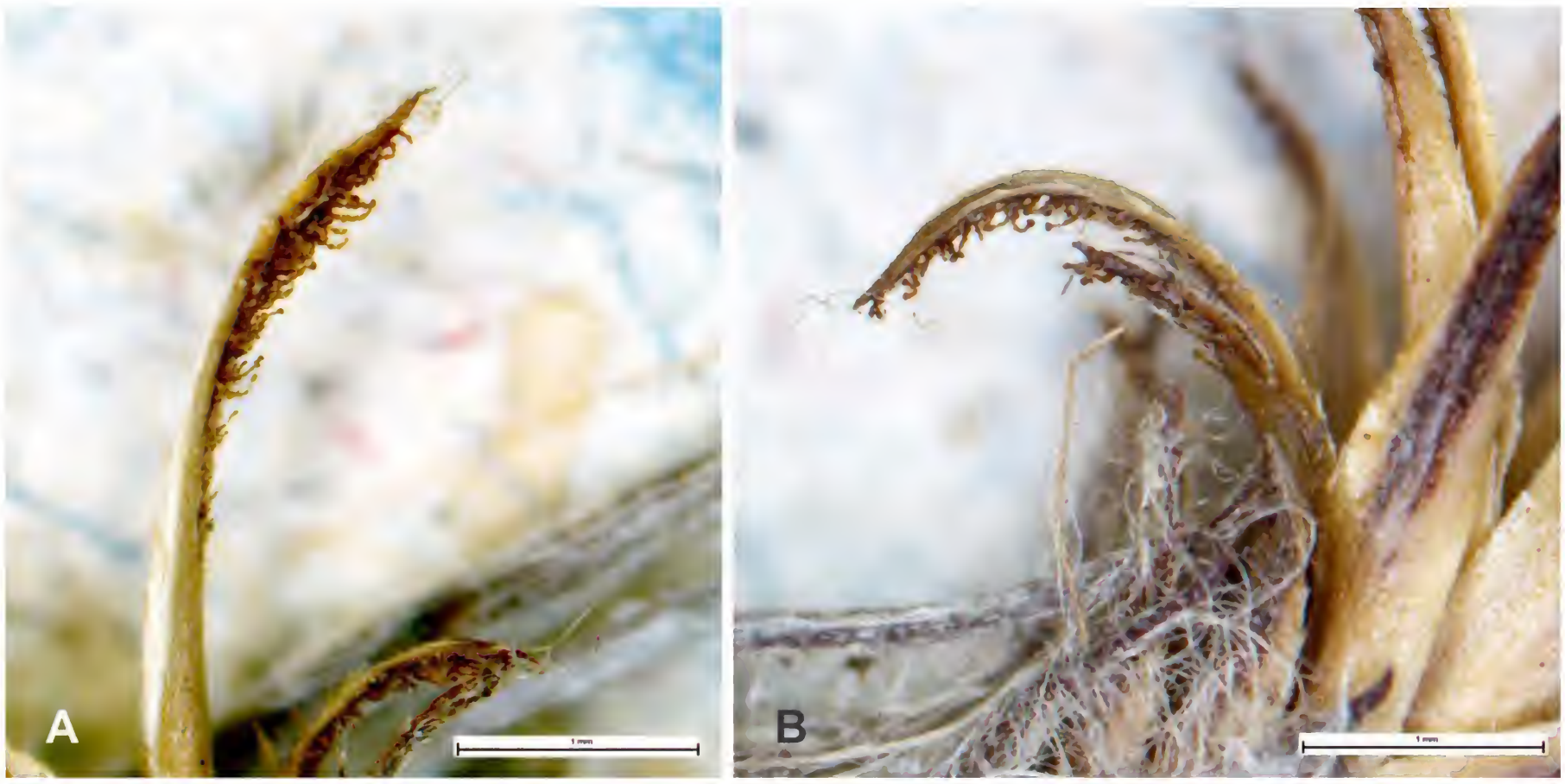
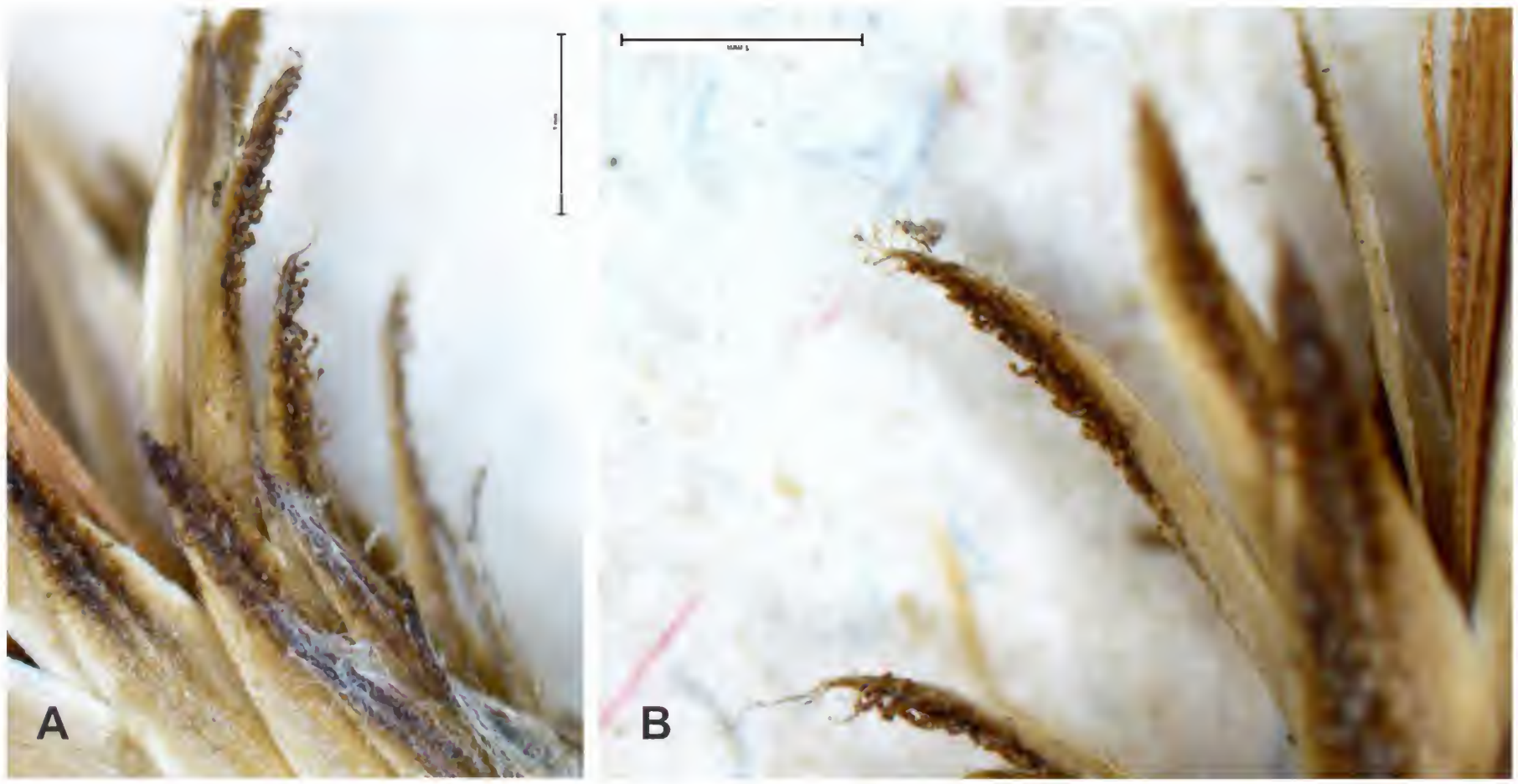


Figure 3. Mixed collection of *Pityopsis latifolia* and *P. microcephala*, *Michaux s.n.* (P00742815) rejected as an isotype of *P. graminifolia*. <http://coldb. mnhn.fr/catalognumber/mnhn/p/p00742815>



Figures 4. Phyllaries details of the holotype of *Inula graminifolia*. Scale bar = 1 mm in A and B



Figures 5. Phyllaries details of the isotype of *Inula graminifolia* (00742818). Scale bar = 1 mm, A and B.

Figures 6. Phyllaries details of the *Pityopsis latifolia* (A) and *P. microcephala* (B); *Michaux s.n.* P00742815. Scale bar = 1 mm in A and B

Nesom, G.L. 2019. Note on the type of *Pityopsis graminifolia* (Asteraceae). Phytoneuron 2019-23: 1. Published 25 April 2019. ISSN 2153 733X

NOTE ON THE TYPE OF *PITYOPSIS GRAMINIFOLIA* (ASTERACEAE)

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The specimens I cited (Nesom 2019, p. 9) for *Inula graminifolia* Michx. (= *Pityopsis graminifolia* (Michx.) Nutt.) as "probable holotype" and "possible isotype" were the only potential type material included at the time in the online database of the MNHN (Paris). Semple and Jabbour (2019) have pointed out that an authentic holotype does exist at P and have provided photos of the plant and critical morphological features (their Figs. 1 and 4).

The specimen identified by Semple and Jabbour as the holotype of *Inula graminifolia* represents the same species as I identified as *Pityopsis graminifolia*, thus clarification of the type does not affect the taxonomic structure that I proposed. A revised nomenclatural/typification summary for *Pityopsis graminifolia* is as follows.

Pityopsis graminifolia (Michx.) Nutt., Trans. Amer. Philos. Soc. 2, 317. 1841. *Inula graminifolia* Michx., Fl. Bor.-Amer. 2: 122. 1803 (before 19 March, fide Schubert 1942). *Chrysopsis graminifolia* (Michx.) Ell., Sketch Bot. S. Carolina 2(4): 334. 1824 [1823], not *C. graminifolia* (Michx.) Nutt. ex Torr. & Gray 1842. *Diplopappus graminifolius* (Michx.) Less., Linnaea 5(1): 144. 1830. *Diplogon graminifolium* (Michx.) Kuntze, Revis. Gen. Pl. 1: 334. 1891. *Heterotheca graminifolia* (Michx.) Shinners, Field & Lab. 19: 71. 1951. **TYPE**: **USA**. "Caroline, fleurit en Septembre," *A. Michaux s.n.* (holotype: P-MICHX without barcode, image!; isotypes: P 00742815 image!, all three stems; P 00742818 image!, middle plant, the 2 outer stems apparently are *Pityopsis microcephala*).

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Semple, J.C. and F. Jabbour. 2019. Type specimens of *Inula (Pityopsis) graminifolia* (Asteraceae: Astereae). Phytoneuron 2019-24: 1–9.

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A MULTIVARIATE MORPHOMETRIC ANALYSIS OF *SOLIDAGO* SUBSECT. *HUMILES* (ASTERACEAE: ASTEREAE)

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ABSTRACT

A multivariate morphometric study of the goldenrod group *Solidago* subsect. *Humiles* was conducted to assess the morphological differences among *Solidago arenicola*, *S. austrocaroliniana*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*. Eleven analyses were performed on different combinations of a priori species groups and traits using a matrix of 170 specimens by 39 traits and provided support for recognizing 13 species. An identification key to all 13 species in *S.* subsect. *Humiles* is included.

Solidago subsect. *Humiles* (Rydb.) Semple includes 5-13 species depending upon the taxonomic treatment (Nesom 1993; Semple and Cook, 2006; Semple and Peirson 2013; Semple 2019 frequently updated): *Solidago arenicola* B.R. Keener & Kral, *S. austrocaroliniana* Semple, *S. bellidifolia* E.L. Greene, *S. chlorolepis* Fern., *S. gillmanii* (A Gray) Steele, *S. glutinosa* Nutt., *S. kralii* Semple, *S. ontarioensis* (Ringius) Semple & J. Peirson, *S. plumosa* Small, *S. racemosa* E.L. Greene, *S. randii* (Porter) Britton, *S. simplex* Kunth, and *S. spathulata* DC. All members of the subsection have some resin on the phyllaries and peduncles and sometimes over much of the plant. The resin is produced by very small stipitate glands that are usually hidden under the resin. Basal rosette and lower stem leaves are generally the largest produced by plants of *S.* subsect. *Humiles*. Early formed rosette leaves are small, spatulate, and petiolate, while later formed rosette leaves can be similar but larger or oblanceolate and tapering to a shorter winged petiolate portion. Upper stem leaves are much reduced. Inflorescences are few to many headed and range from semi-corybiform in very small plants to narrowly to broadly paniculiform in most plants.

Peirson et al. (2013) looked at cpDNA haplotype variation using spatial analysis of molecular variance in 11 taxa in *S.* subsect. *Humiles* following the nomenclature of Semple and Cook (2006) but recognized here at the species level. Samples of *S. austrocaroliniana*, *S. bellidifolia*, and *S. chlorolepis* were not included. Peirson et al. (2013) concluded that "cpDNA variation was not strongly partitioned across species boundaries, geography or ploidy levels", that the "highest haplotype diversity was located in western North America, followed by the southeastern USA and the formerly glaciated Great Lakes region", and "six haplotypes were shared among species in *Solidago* subsect. *Humiles*". Of note, the *S. simplex* sample from Mexico had a unique haplotype (arbitrarily assigned no. 46) which was placed in the parsimony network in a grouping with haplotypes radiating from haplotype 21, which also occurred in samples from the central Rocky Mts., and the southeastern US and was in turn connected to haplo group 4 common in eastern North America and one sample from British Columbia in western North America (Peirson et al. 2013, their Fig. 2). Peirson et al. (2018) also concluded that their "demographic analyses placed the main population expansion in *S.*

subsect. *Humiles* between the late Pleistocene and early Pliocene (well before the Wisconsinan glacial period hypothesis of Ringius & Semple, 1987)" but "also support the evolution of polyploid taxa within a Holocene timeframe". Semple (2016) placed *S.* subsect. *Humiles* in a close relationship with subsect. *Multiradiatae* Semple native to North America and subsect. *Solidago* native to Eurasia.

Species in *S.* subsect. *Humiles* can be morphologically similar but have some critical differences. *Solidago arenicola* has large heads in a very open inflorescence (Figs. 1 and 2); cypselae are glabrous. *Solidago austrocaroliniana* is similar to *S. arenicola* in general appearance but has smaller involucres and blooms in the late spring (see Figs. 1 and 2 in Semple and Nelson 2018); cypselae are glabrous. *Solidago bellidifolia* includes short alpine plants with obviously spatulate rosette and lower stem leaves (Fig.3); cypselae are moderately to moderately-densely strigose. *Solidago chlorolepis* includes small plants with small heads (Fig. 4); cypselae are moderately densely strigose. *Solidago gillmanii* includes mid size to large plants with large serrate, acute, lanceolate basal and lower stem leaves, stems that are glabrate to moderately short hairy and larger heads (Figs. 5 and 6); the cypselae are moderately to densely short-strigose both proximally and distally. *Solidago glutinosa* includes small to mid size plants depending upon growing conditions and elevation (Figs. 7 and 8; see also Semple et al. 2016 Fig. 3); cypselae are moderately to moderately densely strigose over entire fruit body or slightly more so distally. In the Rocky Mountains, higher elevation plants of *S. glutinosa* can be confused with plants of *S. multiradiata* Ait. that mostly have broadly lanceolate to ovate leaves with long ciliate hairs on the margins and phyllaries that are lanceolate, attenuate and often subequal. *Solidago kralii* can be robust with many shoots from a single rootstock or much less robust with a single mid size stem (Figs. 9 and 10), and peduncles have 4-5 bracts; cypselae are glabrous. *Solidago ontarioensis* includes small to mid size plants with small compact to more open inflorescences (Figs. 11 and 12); cypselae tend to be rather strigose. *Solidago plumosa* can be similar to *S. kralii*, but the shoots are often smaller (Figs. 13 and 14), the leaves are narrower, and peduncles have 4-7 bracts; cypselae are glabrous. *Solidago racemosa* varies greatly in stem height depending upon whether rootstocks are growing in small cracks in rocks or in large ones with more soil or in rocky soil; stem leaves tend to be narrowly lanceolate and sharply acute and sometimes numerous (Figs. 15 and 16); cypselae are glabrate to sparsely strigose proximally and very sparsely to moderately strigose distally. *Solidago randii* includes small to robust plants with generally broadly lanceolate, serrate lower leaves with petioles that are broadly winged distally to less so proximally (Figs. 17-19); cypselae are very sparsely proximally to sparsely so distally to sparsely proximally to moderately so distally. *Solidago simplex* are generally small to midsize plants with heads with broad phyllaries for the subsection; phyllaries (Fig. 20; see Figs. 1 and 2 in Semple, Ma and Tong 2016); cypselae are glabrous to sparsely strigose. *Solidago spathulata* includes plants with often obviously resinous stems and leaves and heads (Figs. 21 and 22); upper stem leaves are generally obviously serrate with more teeth than other species; cypselae are moderately densely strigose.

The distributions of the thirteen species are allopatric to partially sympatric with one or more other species in the subsection (Figs 23 and 24). The most widely distributed species is *S. glutinosa* occurring from Alaska to Arizona and New Mexico in the Rocky Mount Cordillera and east across Canada to Ontario and northern Michigan (Fig. 23). *Solidago simplex* occurs in the central Sierra Madre Oriental of east-central Mexico (Fig. 23). *Solidago bellidifolia* occurs at higher elevations in the northern Cascade Mountains of northern Oregon, western Washington and Vancouver Island, British Columbia (Fig. 23). All other species occur is mostly allopatric disjunction populations in eastern North America. *Solidago ontarioensi*s is confined to the islands and the mainland near Lake Huron and eastern Lake Superior (Fig. 24) in rocky soils and cracks in limestone and gneiss outcrops. *Solidago gillmanii* occurs in sandy soils along the eastern and northern shores of Lake Michigan and a few locations in northern Lake Huron (Fig 24). *Solidago randii* occurs in rocky soils in upland areas

Figure 1. Robust shoot of *Solidago arenicola*, *Semple & B. Semple 11196* (WAT) from Alabama.

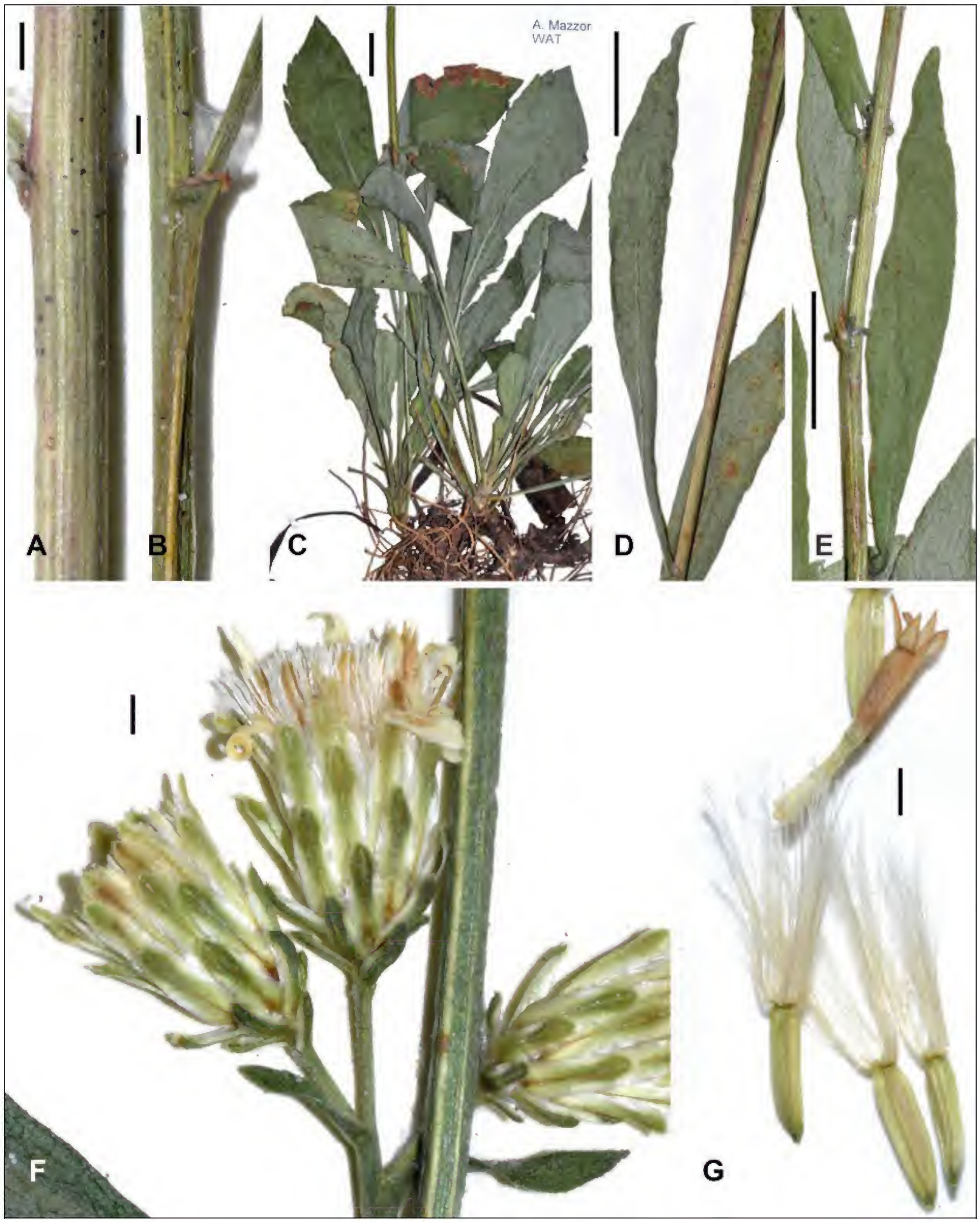

Figure 2. Details of the morphology of *Solidago arenicola*. **A.** Lower stem, *J. & B. Semple 11296* (WAT). **B.** Stem in inflorescence, *J. & B. Semple 11293* (WAT). **C.** Basal rosette and lower stem leaves, *J. & B. Semple 11291* (WAT). **D-E.** Mid and upper stem leaves, *J. & B. Semple 11296* (WAT). **F.** Heads, *J. & B. Semple 11291* (WAT). **G.** Disc floret cypselae, *J. & B. Semple 11293* (WAT). Scale bars = 1 mm in A-B, and F-G; = 1 cm in C-E.

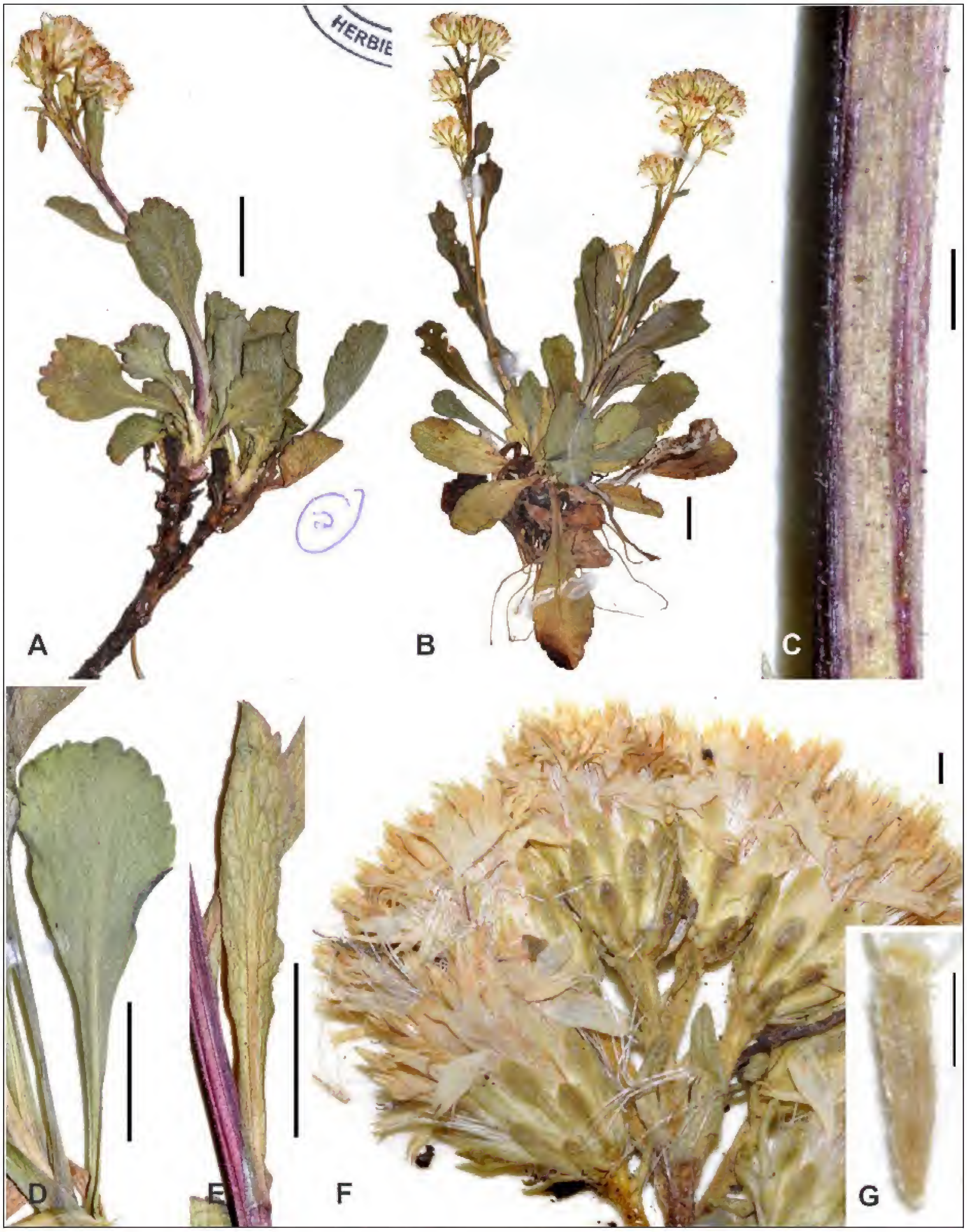

Figure 3. Morphology of *Solidago bellidifolia*. **A.** Mt. Hood, Oregon; *Semple & Xiang 10270* (WAT). **B.** Vancouver Is., British Columbia, Ceska s.n. (V). **C-D.** Lower stem and lower stem leaf, *Ceska s.n.* (V). **E.** Mid stem leaf, *Hardy s.n.* (V). **F.** Heads, *Ceska s.n.* (V). **G.** Cypselae body, *Semple & Xiang 10270* (WAT). Scale bars = 1 mm in C and F-G; = 1 cm in A-B, D-E.

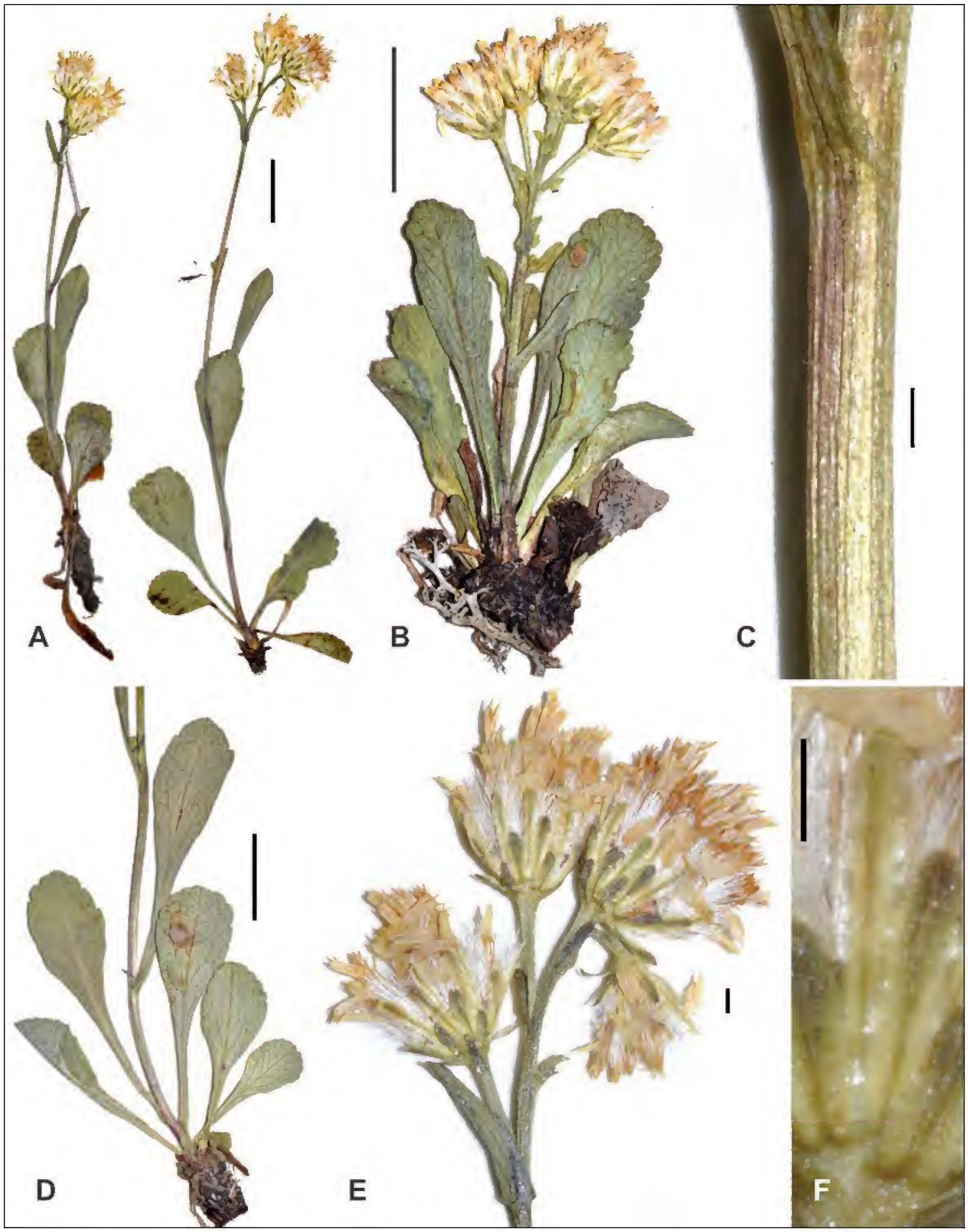

Figure 4. Morphology of *Solidago chlorolepis* from Mt. Albert, Québec. **A**. *Ringius 1694* (WAT). **B.** *Ringius 1700* (WAT). **C.** Mid stem, *Ringius 1691* (WAT). **D.** Lower stem leaves, *Ringius 1704* (WAT). **E-F.** Heads and phyllaries, *Ringius 1694* (WAT). Scale bars = 1 mm in C and E-F; = 1 cm in A-B, D.

Figure 5. *Solidago gillmanii*, *Morton & Venn NA9493* (TRT), Manitoulin Dist., Ontario.

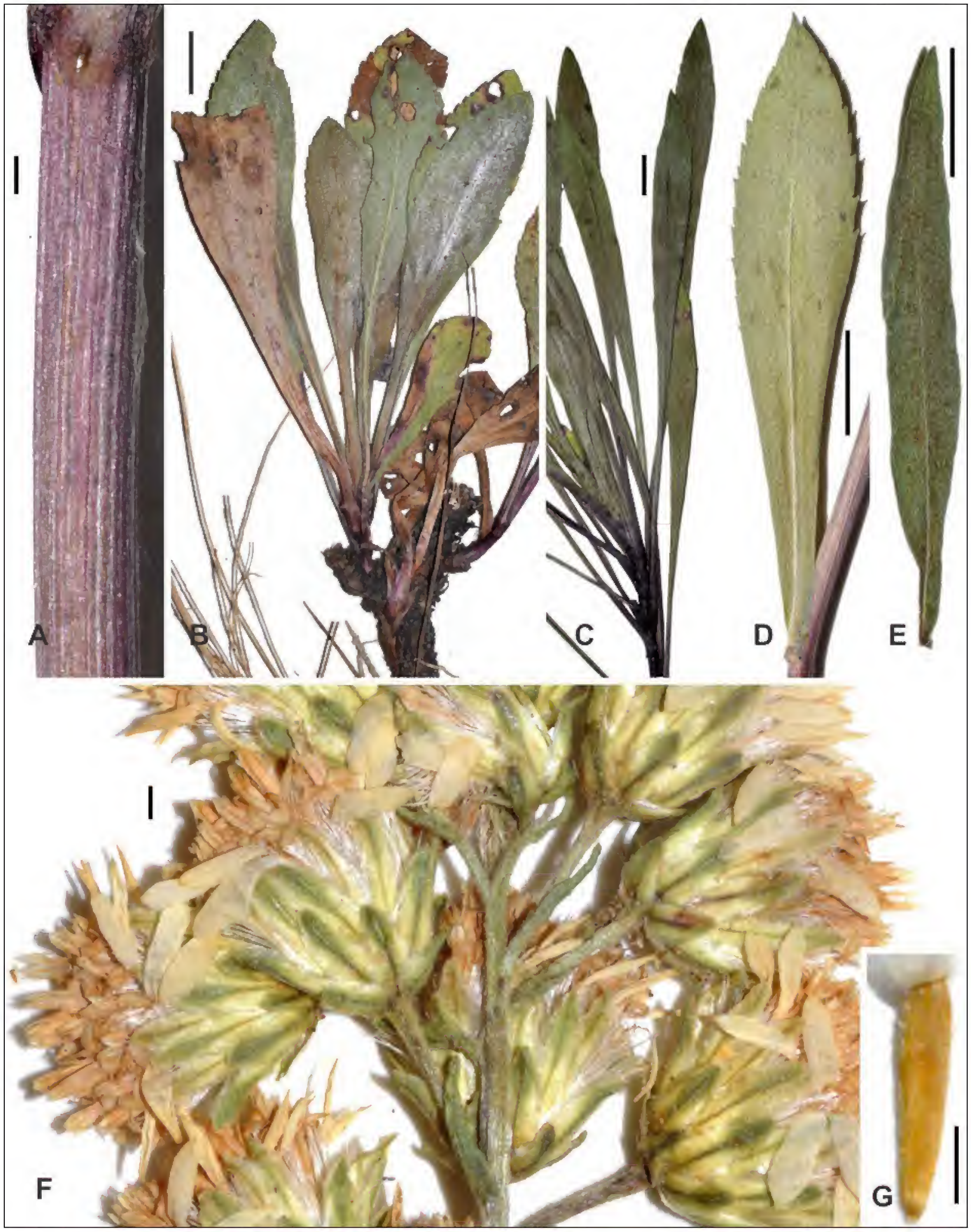

Figure 6. Details of the morphology of *Solidago gillmanii* from Michigan. A. Lower stem, *Ringius 1830* (WAT). **B.** Rosette leaves, *Ringius 1822* (WAT). **C**. Lower stem leaves, *Semple 11842* (WAT). **D.** Mid stem leaf, *Ringius 1830* (WAT). **E.** Upper stem leaf, *Semple 11843B* (WAT). **F.** Heads, *Ringius 1828* (WAT). **G.** Disc floret cypsela body, *Morton & Venn NA10911* (TRT). Scale bar = 1 mm in A and F-G; = 1 cm in B-E.

Figure 7. A robust individual of *Solidago glutinosa, Pavlick 80-431 (V), British Columbia.*

Figure 8. Details of the morphology of *Solidago glutinosa*. **A.** Alpine dwarf, Colorado, *Russell 66-129* (WAT). **B-C.** Lower and mid stem, *Semple & Brouillet 4218* (WAT). **D.** Mid stem, *Chmielewski et al. CCC4470* (WAT). **E-F.** Basal leaves and mid stem leaf, *Chmielewski et al. CCC4470* (WAT). **G.** Upper stem leaf, *Semple & Xiang 102011* (WAT). **H.** Upper stem and leaf, *J. & B. Semple 6556* (WAT). **I.** Heads, *Semple et al. 9370* (WAT). **J-K.** Densely and moderately strigose ovaries/immature cypsela bodies, *Montague & Montague 35* (WTU) and *Zika 22787* (WTU). Scale bars = 1 mm in B-D, and I-K; = 1 cm in C, A, E-H.

Figure 9. *Solidago kralii*. *Semple & B. Semple 11217* (BRIT), Richmond Co., Georgia.

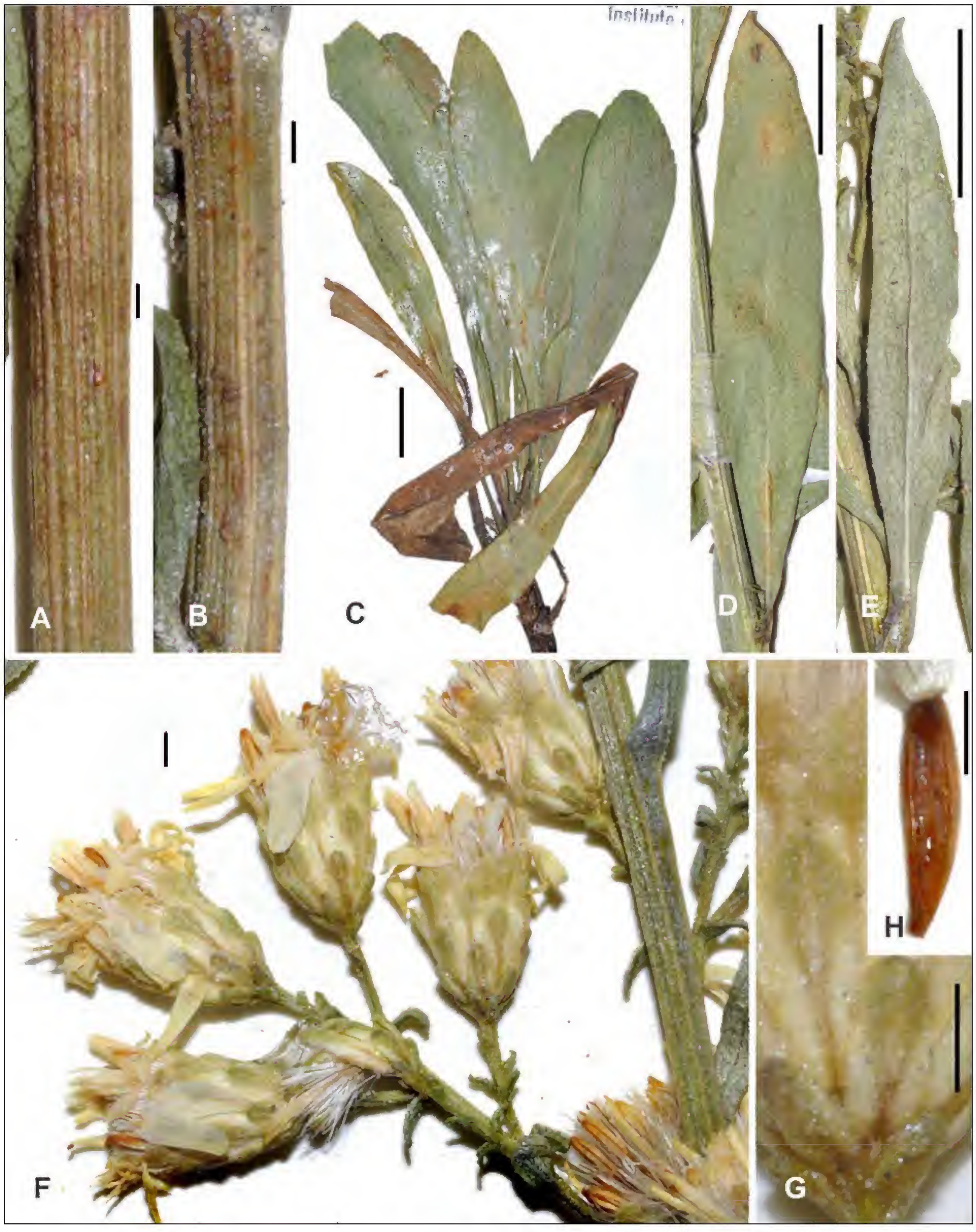

Figure 10. Details of the morphology of *Solidago kralii* from Georgia. **A.** Lower stem, *J. & B. Semple 11208* (WAT). **B.** Upper stem, *J. & B. Semple 11217* (WAT). **C-D.** Rosette leaves and mid stem leaf, *J. & B. Semple 11218* (BRIT). **E.** Upper stem leaf, *J. & B. Semple 11217* (BRIT). **F-G.** Heads and phyllaries, *J. & B. Semple 11217* (WAT and BRIT, respectively). **H.** Disc floret cypsela body, *Jones 15123* (USF). Scale bars = 1 mm in A-B and F-H; = 1 cm in C-E.

Figure 11. *Solidago ontarioensis*, *Morton & Venn NA6350* (TRT), Ontario.

Figure 12. Details of the morphology of *Solidago ontarioensis*. **A.** Small plant, *Morton & Venn NA10586* (TRT). **B.** Lower mid stem, *Morton & Venn NA8061* (TRT). **C.** Mid stem, *Ringius 1448* (WAT). **D.** Basal rosette leaves, *Semple & Brammall 2780* (WAT). **E.** Lower stem leaf blade, *Semple & Brammall 2788* (WAT). **F.** Mid stem leaf, *Ringius 1448* (WAT). **G.** Heads, *Semple & Brammall 2780* (WAT). **H.** Disc floret cypselae, *Morton & Venn NA6350* (TRT). Scale bars = 1 mm in B-C and G-H; = 1 cm in A, and D-F.

Figure 13. *Solidago plumosa*, *J.K. Small s.n.* (MO), Stanley Co., North Carolina.

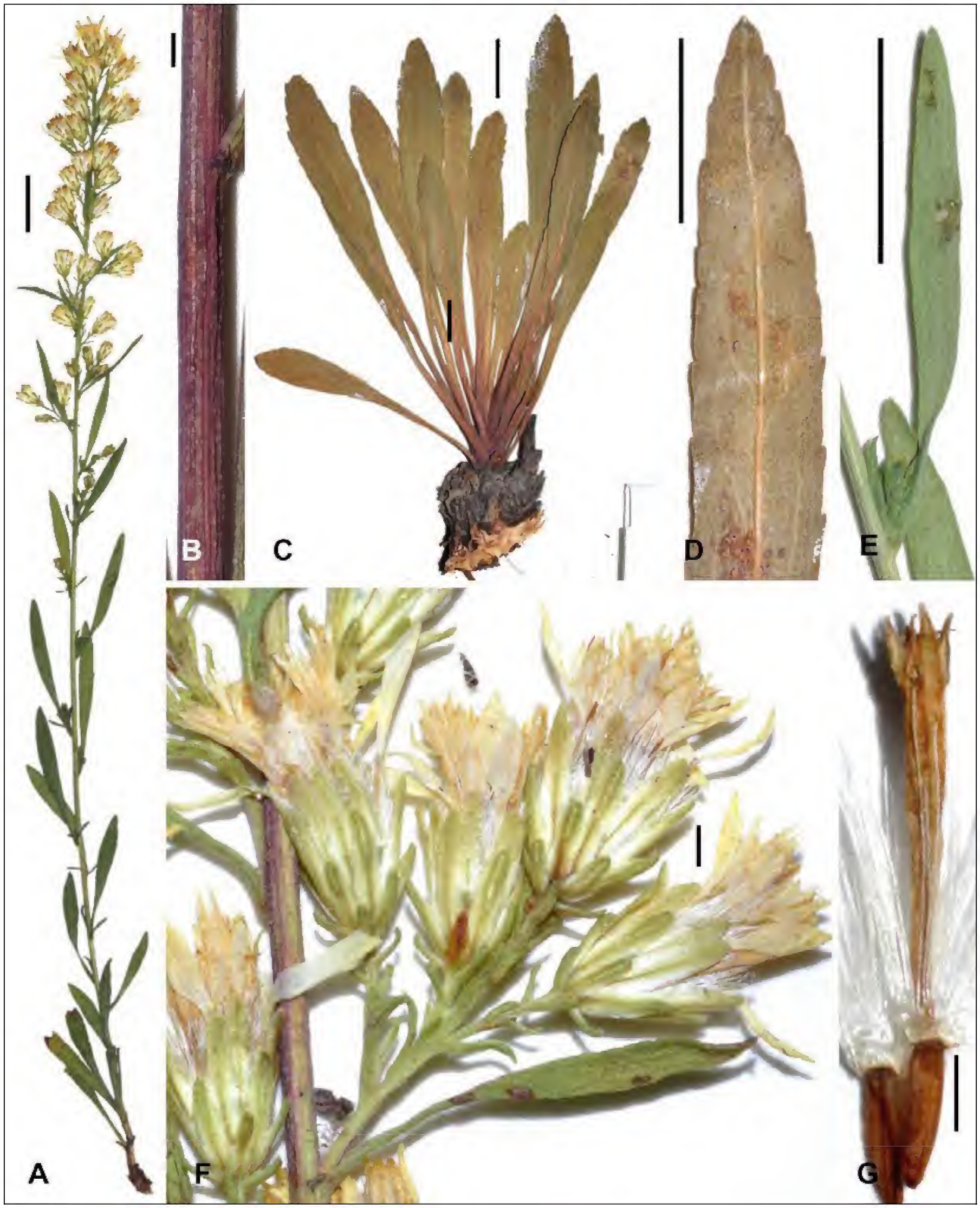

Figure 14. Details of the morphology of *Solidago plumosa*. **A.** Small shoot, *Peirson 604B* (MICH). **B.** Lower stem, *Peirson 604A* (MICH). **C-D.** Basal rosette leaves and detail of apex, *J.K. Small s.n.* (MO). E. Upper stem leaf, Peirson 604B (MICH). **F.** Heads, *Peirson 604A* (MICH). **G.** Disc floret cypselae, *J.K. Small s.n.* (MO). Scale bars = 1 mm in B and F-G; = 1 cm in A and C-E.

Figure 15. Robust *Solidago racemosa*, *Ringius 1721* (WAT) from York Co., New Brunswick.

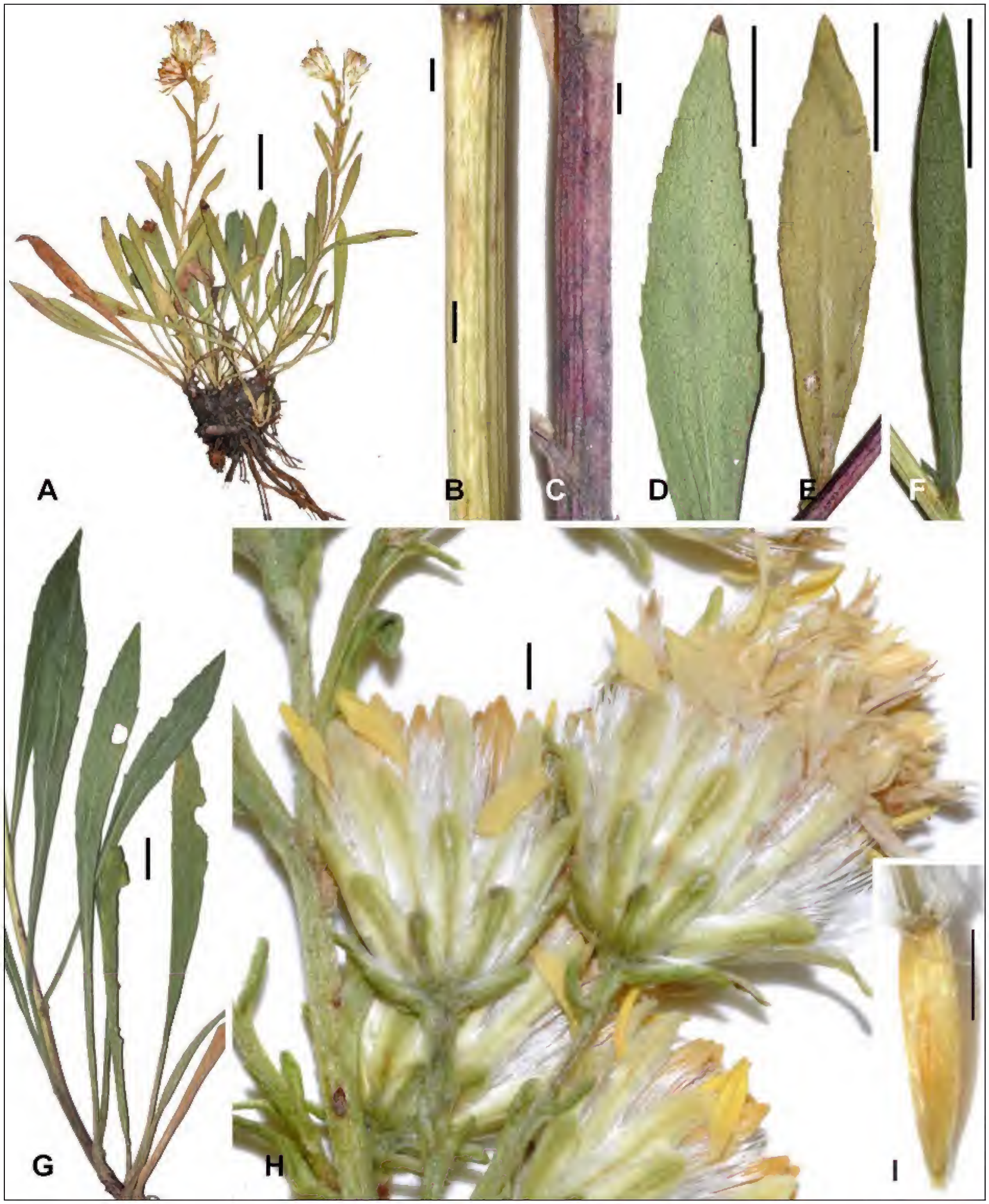

Figure 16. Details of the morphology of *Solidago racemosa*. **A.** Dwarf shoot, *Semple & Ringius 7612* (WAT). **B-C.** Lower stems, *Peirson 597* (MICH) and *Semple & Ringius 7612* (WAT). **D.** Lower stem leaf, *Semple & Ringius 7663* (WAT). **E.** Mid stem leaf, *Gagnon 5059* (QUE). **F-G.** Upper mid stem leaf and lower stem leaves, *Peirson 597* (MICH). **H.** Heads, *Peirson 601* (MICH). **I.** Disc floret cypsela body, *Semple & Ringius 7663* (WAT). Scale bars = 1 mm in B-C, and H-I; = 1 cm in A and D-G.

Figure 17. Robust *Solidago randii*. *Pringle s.n.* (NY), White Mountain Notch, New Hampshire.

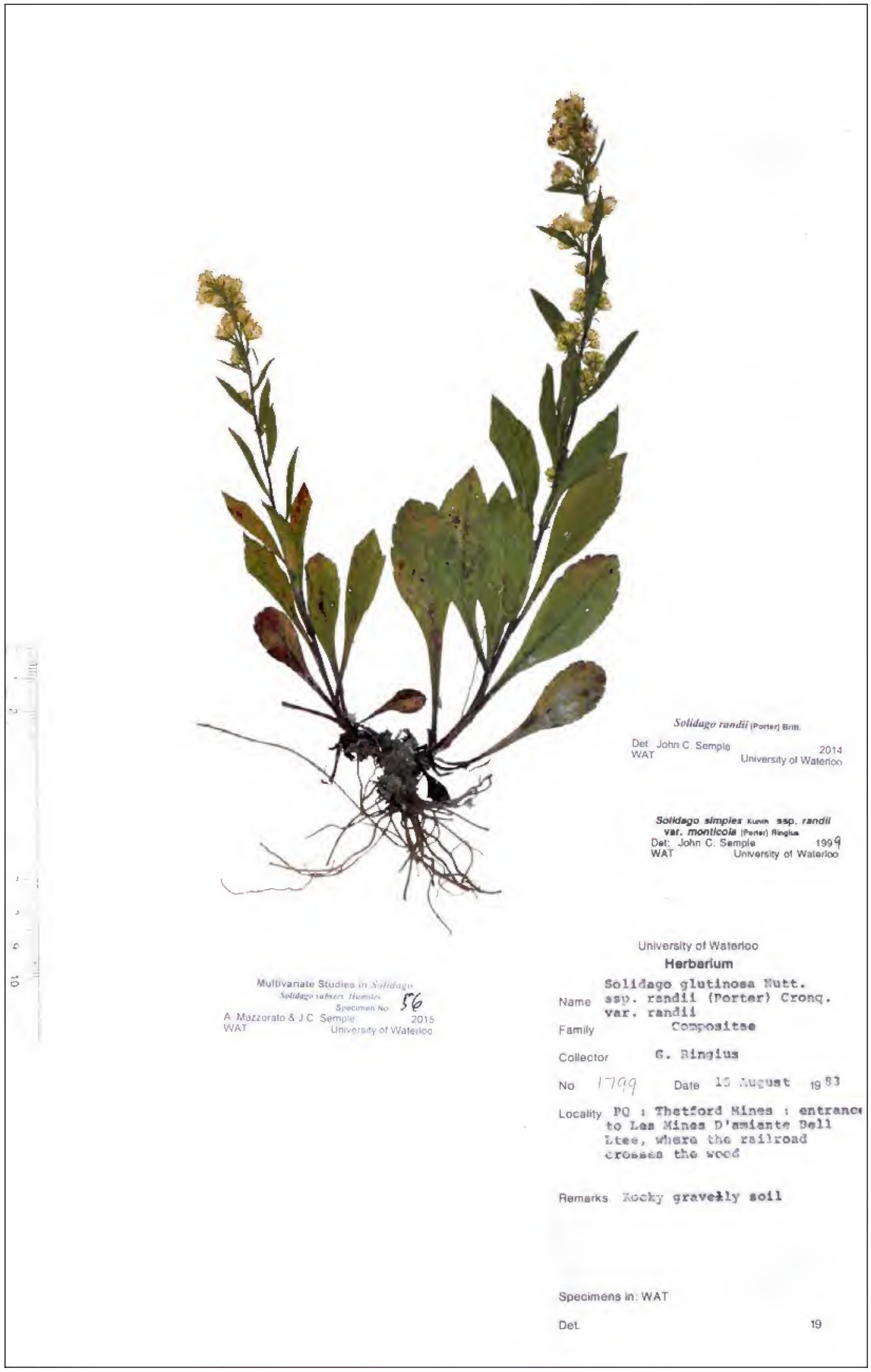

Figure 18. *Solidago randii*. *Ringius 1799* (WAT), Thetford Mines, Québec.

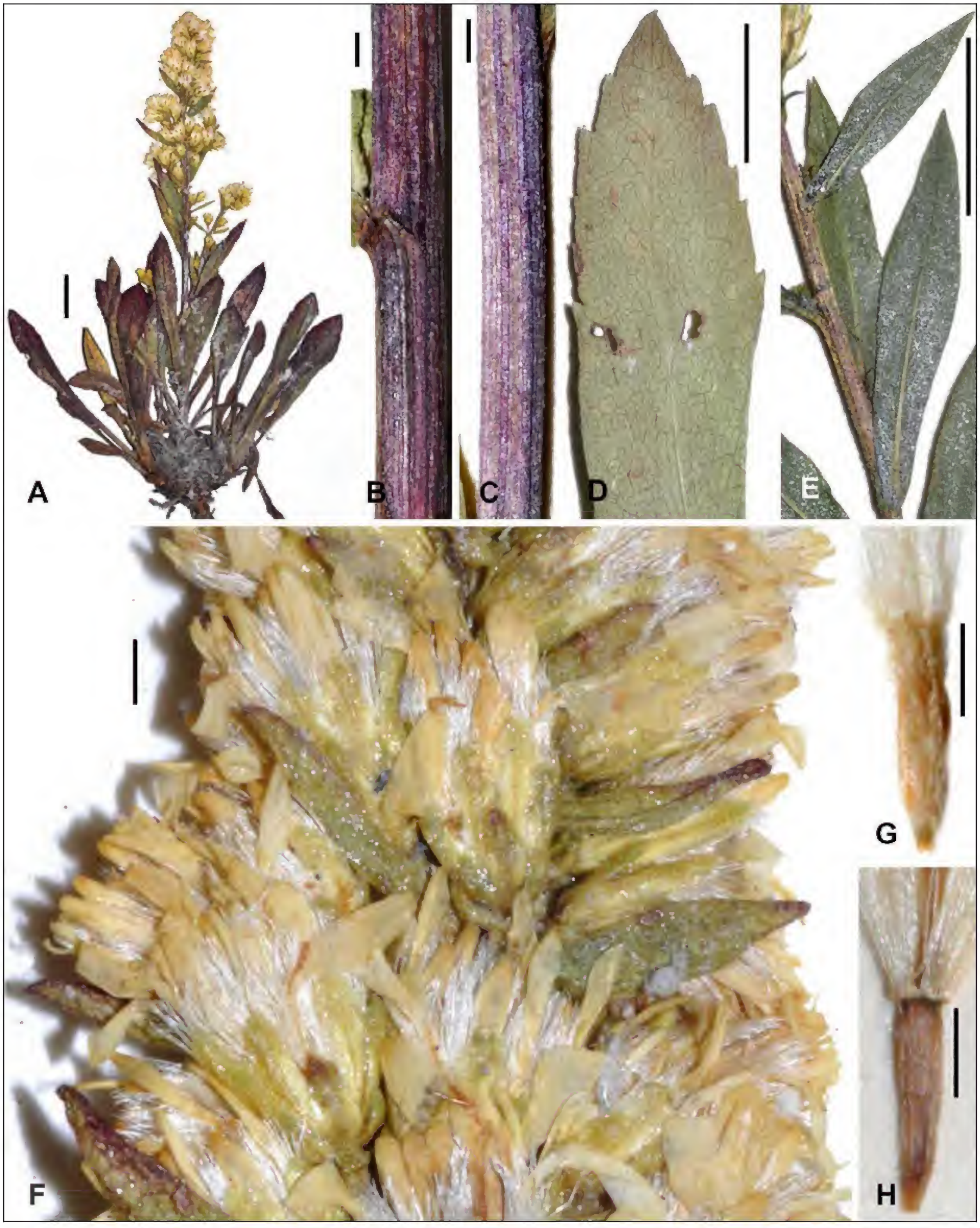

Figure 19. Details of the morphology of *Solidago randii*. **A.** Dwarf shoot, *Ringius 1800* (WAT). **B-C.** Lower and mid stems, *Marie-Victorin et al. 46678* (MT). **D.** Lower stem leaf distal blade, *Ringius 1807* (WAT). **E.** Resinous upper stem leaves, *Ringius 1763* (WAT). **F.** Heads, *Ringius 1800* (WAT). **G-H.** Disc floret cypselae, *Pringle s.n.* (NY) and *Grout s.n.* (NY). Scale bars = 1 mm in B-C and F-G; = 1 cm in A, D-E.

Figure 20. *Solidago simplex*, *Hinton et al. 22120* (TEX), Mpio. Zaragoza, Nuevo Leon, Mexico.

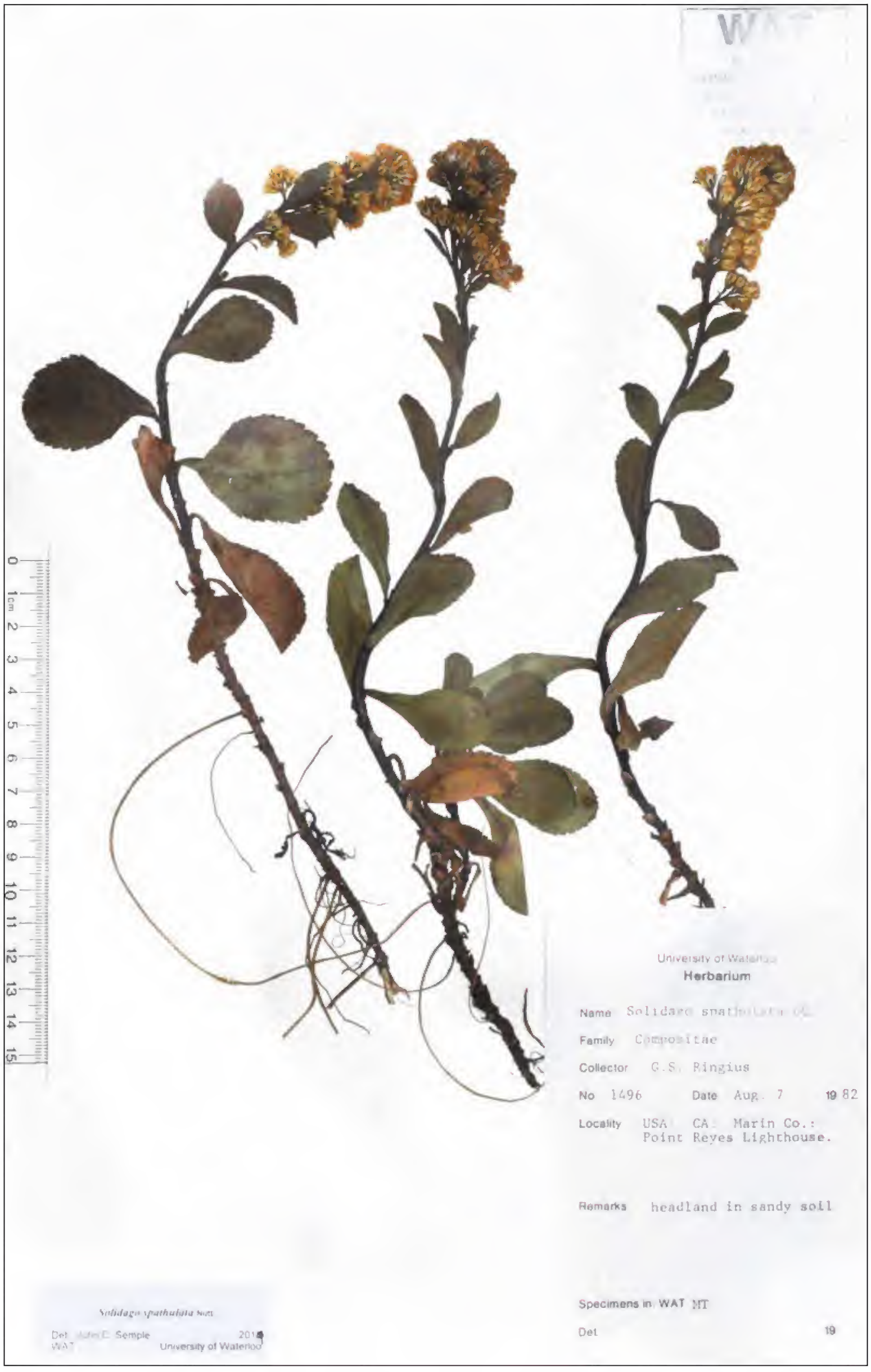

Figure 21. *Solidago spathulata*, *Ringius 1496* (WAT), Marin Co., California.

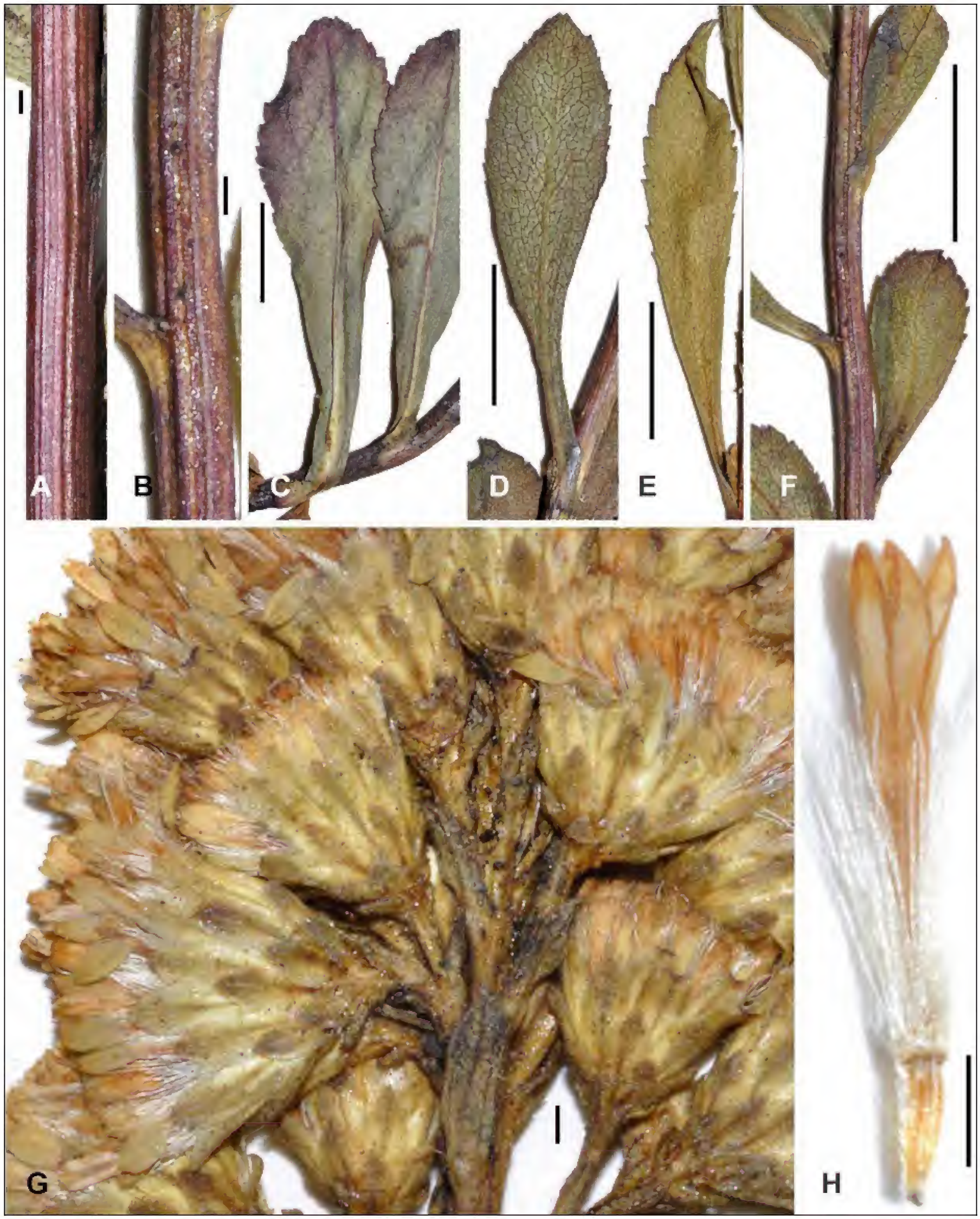

Figure 22. Details of the morphology of *Solidago spathulata.* **A.** Lower stem, *Morton & Venn NA15791* (TRT). **B.** Mid stem, *Ringius 1499* (WAT). **C.** Lower stem leaves, *Ringius 1501*-2 (WAT). **D.** Upper mid stem leaf, *Semple & Heard 8465* (WAT). **E.** Upper stem leaf, *Ringius 1499 (WAT).* **F.** Upper mid stem, *Semple & Heard 8651* (WAT). **G.** Heads, *Ringius 1499* (WAT). Scale bars = 1 mm in A-B, and G; = 1 cm in C-F.

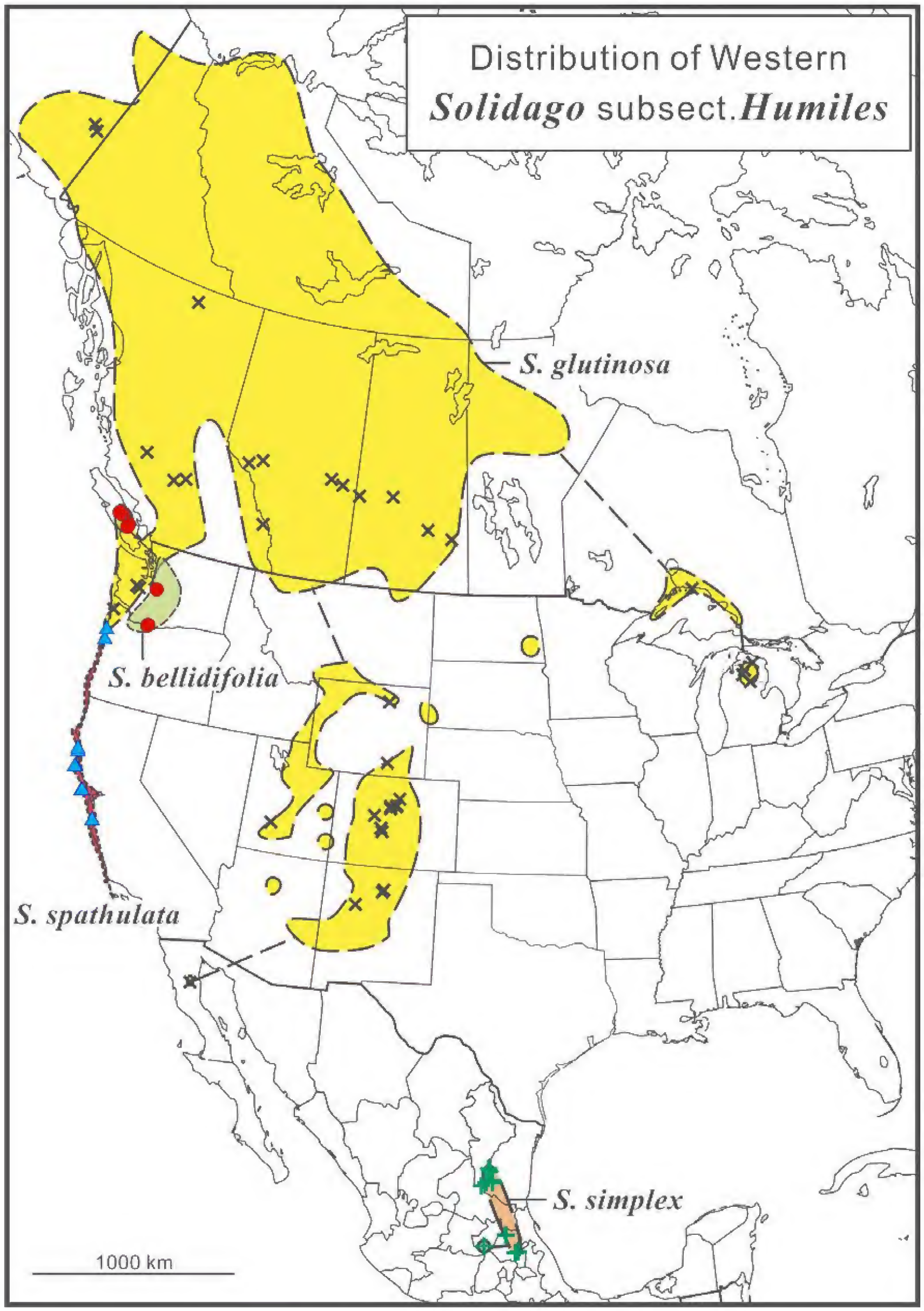

Figure 23. Ranges of distribution of western North American species and locations of samples included in analyses of *Solidago* subsect. *Humiles*; ranges based on all collections seen and literature.

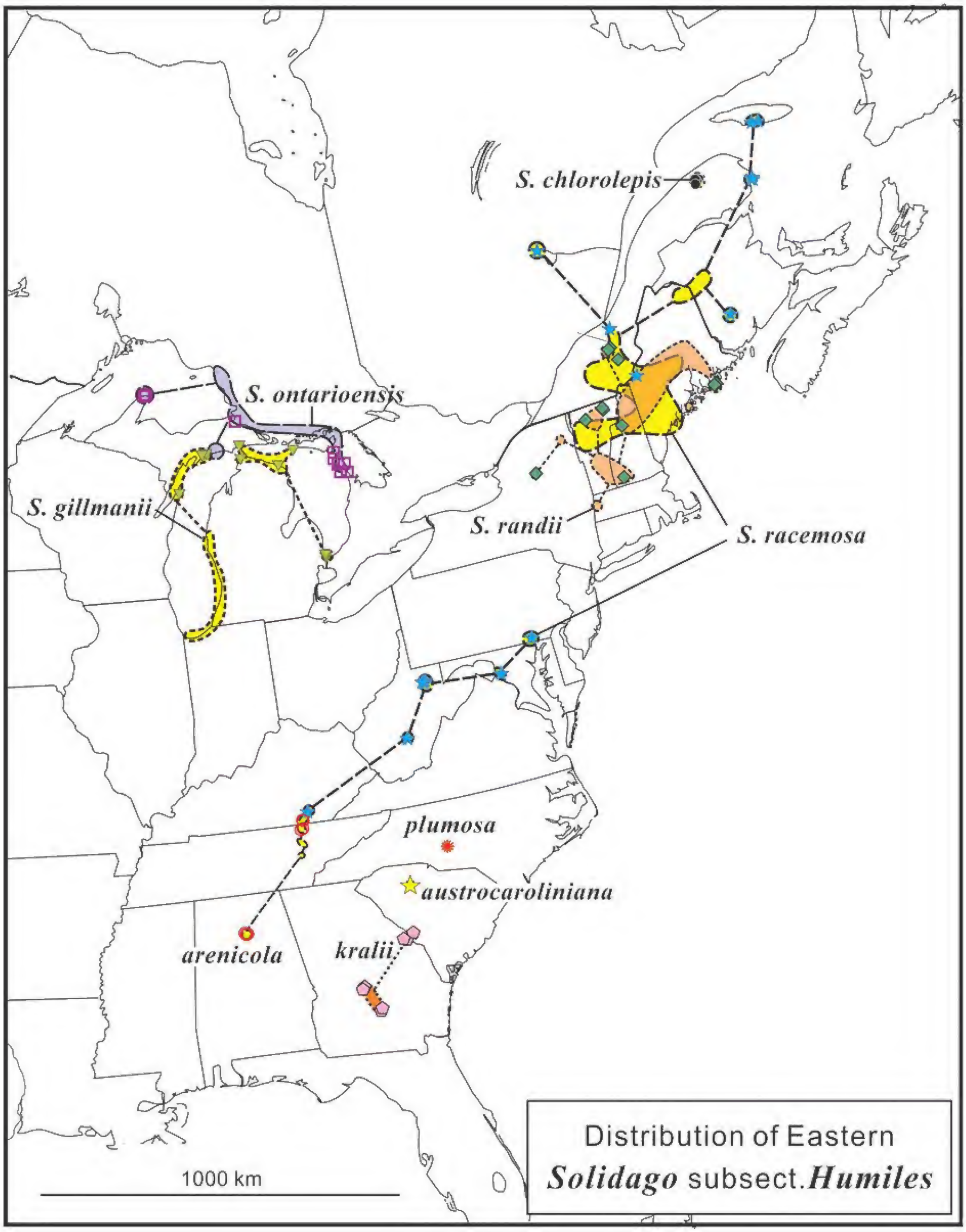

Figure 24. Ranges of distribution of eastern North American species and locations of samples included in analyses of *Solidago* subsect. *Humiles*; range based on all collections seen.

of northern New England, adjacent New York, eastern Québec, and northwestern New Brunswick (Fig 24). *Solidago racemosa* occurs in cracks in rocks and rocky soils along streams and rivers in scattered locations from Anticosti Island in Québec south through New England to Pennsylvania, Maryland, West Virginia, and Kentucky (Fig. 24). The other five species are rare to extremely rare. *Solidago chlorolepis* occurs at higher elevations on Mt. Albert and adjacent peaks in the Gaspé region of Québec (Fig. 24). The other four occur in the southeastern U.S. *Solidago arenicola* occurs in sandy soils along rivers in southern Kentucky and adjacent Tennessee and in northern Alabama (Fig. 24). *Solidago kralii* occurs in sandy soils of the Fall Line counties in Georgia and just into South Carolina (Fig. 24). *Solidago plumosa* occurs in one location on rock outcrops along the Yadkin R., in North Carolina (Fig. 24). *Solidago austrocaroliniana* is known from a single collection from Union Co., South Carolina and is the only species that blooms in the late spring (Fig. 24).

Numerous chromosome number reports have been published for taxa in *Solidago* subsect. *Humiles*, including diploids $2n=9_{II}$ or 2n=18, tetraploids $2n=18_{II}$ or $2n=36$, and hexaploids $2n=54$. *Solidago bellidifolia, S. spathulata, S. chlorolepis, S. kralii,* and *S. plumosa* have been reported to be diploid one to multiple times (Ringius and Semple 1987; Peirson et al. 2012 including references to previously published counts). Solidago *glutinosa* is diploid throughout its range with infrequent tetraploids having been reported from only northern Michigan (Peirson et al. 2012). *Solidago arenicola*, *S. gillmanii*, *S. ontarioensis*, *S. racemosa*, and *S. randii* are tetraploid with multiple counts for each species (Peirson et al. 2012). Hexaploids have been reported twice for *S. racemosa* (Beaudry 1963; Peirson et al. 2012). No counts have been reported for *S. austrocaroliniana* and *S. simplex*.

The purpose of this study was to the determine statistical support for recognizing the species and subspecies/varieties proposed within *Solidago* subsect. *Humiles*, the levels of distinctiveness among the taxa, and what technical traits could be used to separate taxa besides those used to define the taxa as groups a priori. No previous study has included all species. Ringius (1986, Ph.D. thesis) compared *S. glutinosa* (with multiple infraspecific taxa) with *S. spathulata* and considered *S. plumosa* to be likely extinct. Rediscovery of *S. plumosa* and publication of *S. austrocaroliniana*, *S. arenicola*, and *S. kralii* subsequently expanded the taxa to be studied. Semple, Ma and Tong (2016) used multivariate statistical methods to demonstrate the distinctiveness of *S. simplex* from Mexico from *S. glutinosa* from Canada and the US. Nesom (1989) had placed *S. glutinosa* into synonymy under *S. simplex* following traditional taxonomic observation methods.

MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria (BRIT, DES, GH, the J.K. Morton personal herbarium now in TRT, KY, LL, MICH, MT, NCU, QUE, TEX, USF, V, WAT in MT, and WTU; Thiers continuously updated). More than 3000 specimens were examined, from which 170 specimens were chosen and measured for the statistical analyses based on completeness of the specimen, maturity, and geographical distribution: 12 specimens of *S. arenicola*, 1 of *S. austrocaroliniana*, 13 of *S. bellidifolia*, 11 of *S. chlorolepis*, 10 of *S. gillmanii*, 34 of *S. glutinosa*, 12 of *S. kralii*, 12 of *S. ontarioensis*, 11 of *S. plumosa*, 18 of *S. racemosa*, 11 of *S. randii*, 11 of *S. simplex*, and 11 of *S. spathulata*. In total, 19 vegetative and 20 floral traits were scored for (Table 1). Additional stem, leaf, inflorescence, and phyllary indument traits were used in assigning specimens to a priori groups.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016) and are not repeated here. Multiple analyses were performed over more than a decade as sample sizes were increased and samples of rarer species became available. In the first analysis, all samples of all species except *S. austrocaroliniana* were included in a STEPWISE discriminant. In the second analysis, all samples of all species except *S. austrocaroliniana* and *S. spathulata* were included in a STEPWISE discriminant. In the third

analysis, only specimens of the four western taxa *S. bellidifolia*, *S. glutinosa*, *S. simplex* and *S. spathulata*, were included in a STEPWISE discriminant. In the fourth, *S. bellidifolia* and *S. glutinosa* were investigated in a STEPWISE analysis. In the fifth, *S. glutinosa* and *S. simplex* were investigated in a STEPWISE analysis. In the sixth and seventh analyses, only specimens of the northeastern taxa *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis, S. racemosa*, and *S. randii* were included in STEPWISE and COMPLETE analyses. In the eighth, only specimens of *S. glutinosa* and *S. ontarioensis* were included a STEPWISE analysis. In the ninth analysis, only specimens of *S. racemosa* and *S. randii* were included a STEPWISE analysis. In the tenth analysis, specimens of the four southeastern taxa *S. arenicola*, *S. kralii*, S. *plumosa*, and *S. racemosa*, were included in a STEPWISE analysis. In the eleventh analysis, only specimens of *S. arenicola* and *S. racemosa* were included a STEPWISE analysis. The single specimen of *S. austrocaroliniana* was included a posteriori in the first, second, and tenth analyses.

Table 1. Traits scored for the multivariate analyses of 170 specimens of *Solidago* subsect. *Humiles*.

Abbreviation	**Description of trait scored**
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
UPSTMNOD25	Number of nodes on the top 25% of the stem below the inflorescence
CAPL	Length of inflorescence (cm)
CAPWD	Width of inflorescence (cm)
CBRNCHLN	Length of longest lower inflorescence branches (cm)
PEDBRCTS	Number of peduncle bracts and location
INVOLHT	Involucre height at anthesis (mm)
OPHYLLN	Outer phyllary length (mm)
MPHYLLN	Middle phyllary length (mm)
MPHYLWD	Middle phyllary width, widest point (mm)
MPHYLWD2	Middle phyllary width 1 mm below tip (mm)
RAYNUM	Number of ray florets per head

RSTRAPLN	Ray lamina length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray lamina width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
RPUB	Density variation of hairs on ray floret ovary/fruit body (0-5 scale)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DPUB	Density variation of hairs on disc floret ovary/fruit body (0-5 scale)

RESULTS

Twelve species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length, upper stem leaf width, and the number of upper stem leaf margin serrations. Basal rosette leaves were sometimes not present and were not included in the analyses. Stem height correlated strongly with basal rosette and lower stem leaf traits and was included as proxy for the lower stem and rosette leaf traits, although in most species stem height was highly variable. Lower stem leaves were present on many specimens but were not included in the analyses because their traits correlated highly among themselves and with mid and upper stem leaf traits. Among the floral traits scored, involucre height and length of the disc corolla were strongly correlated as were ray floret lamina width and disc corolla lobe length, ray and disc floret ovary/fruit body lengths, ray and disc floret pappus lengths at anthesis, and ray and disc floret ovary/fruit body hair densities.

In the STEPWISE discriminant analysis of 168 specimens of twelve species level a priori groups (*Solidago arenicola*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*), the following eight traits were selected and are listed in order of decreasing F-to-remove values: number of upper stem leaf margin serrations (23.33), stem height (11.53), number of peduncle bracts (10.95), involucre height (9.22), number of ray florets (8.34), upper stem leaf width (5.73), mid stem leaf length (5.66), and mid series phyllary width (5.60). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. plumosa* and *S. spathulata* (41.146); the smallest separations were between *S. bellidifolia* and *S. chlorolepis* (0.747) and between *S. glutinosa* and *S. randii* (1.884).

In the Classificatory Discriminant Analysis of 168 specimens of the twelve species level a priori groups (*Solidago arenicola*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*) plus 1 specimen of *S. austrocaroliniana* include a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 53-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Ten of the 10 specimens of the *S. plumosa* a priori group (100%) were assigned a posteriori to *S. plumosa*: 9 specimens with 98-100% probability and 1 specimen with 79% probability. Eleven of the 12 specimens of the *S. arenicola* a priori group (92%) were assigned a posteriori into the *S. arenicola* group: 9 specimens with 96-100% probability and 2 specimens with 66% and 63% probability. One

Table 2. Between groups F-matrix for the twelve a priori groups in a STEPWISE analysis (df = 8 149)

Group	*areni-cola*	*bellidi-folia*	*chloro-lepis*	*gill-manii*	*glutin-osa*	*kralii*	*ontario-ensis*	*plum-osa*	*racem-osa*	*randii*	*simplex*
bellidifolia	26.518										
chlorolepis	25.668	0.747									
gillmanii	11.472	10.784	11.142								
glutinosa	32.939	6.791	4.722	13.220							
kralii	12.884	30.121	26.779	13.104	27.433						
ontarioensis	16.302	4.385	3.897	8.446	2.506	21.133					
plumosa	16.729	33.445	27.442	25.590	33.596	12.173	24.143				
racemosa	9.510	10.375	10.131	11.158	13.074	16.540	6.442	17.220			
randii	26.559	5.013	3.361	12.493	1.884	19.948	3.873	26.567	9.419		
simplex	15.462	6.849	6.243	7.236	4.810	11.872	3.415	23.059	7.727	2.834	
spathulata	38.441	26.764	25.670	27.743	31.300	34.733	23.277	41.146	31.156	28.510	24.081

Lambda = 0.0056 df= 8 11 156; Approx. F=13.4979 df = 88 986 prob = 0.0000

specimen of the *S. arenicola* a priori group was assigned a posteriori to *S. racemosa* with 36% probability (19% to *S. simplex*, 17% to *S. ontarioensis*, 8% to *S. arenicola,* and 6% to *S. plumosa* (*Bailey B150* WAT from Scott Co., Tennessee; nearly all heads were immature). Ten of the 11 specimens of the Mexican *S. simplex* a priori group (91%) were assigned a posteriori to *S. simplex*; 2 specimens with 98% and 93% probabilities, 1 specimen with 87% probability, 2 specimens with 72% and 66% probabilities, 2 specimens with 55% (24% to *S. gillmanii*) and 51% probability (32% to *S. randii*), and 3 specimens with 44% probability (33% to *S. randii* and 11% to *S. glutinosa*), 33% probability (31% to *S. randii* and 14% to *S. glutinosa*) and 33% probability (28% to *S. gillmanii* and 22% to *S. racemosa*). One specimen of the *S. simplex* a priori group was assigned a posteriori to *S. randii* with 41% probability. Nine of the 10 specimens the *S. gillmanii* a priori group (90%) were assigned a posteriori to *S. gillmanii*; 5 specimens with 91-100% probability and 4 specimens with 81-89% probability. One specimen of the *S. gillmanii* a priori group was assigned a posteriori to *S. chlorolepsis* with 23% probability (20% to *S. gillmanii,* 18% to *S. bellidifolia*, 14% to *S. ontarioensis*, 14% to *S. glutinosa* and 6% to *S. randii*; *Ringius 1851* WAT from Door Co., Wisconsin). Ten of 12 specimens of the *S. spathulata* a priori group (83%) were assigned a posteriori to *S. spathulata*; 9 specimens with 100% probability and 1 specimen with 82% probability. Two specimens of the *S. spathulata* a priori group were assigned a posteriori to other species: 1 specimen to *S. glutinosa* with 54% probability (*Morton NA3312* TRT from Newport, Oregon; upper stem leaves had multiple margin serrations and the involucres had a thick shiny resinous coating usual for of *S. spathulata*) and 1 specimen to *S. simplex* with 29% probability (26% to *S. gillmanii*, and 10% to *S. glutinosa*; *Semple & Heard 8541* WAT from Medocino Co., California). Nine of 11 specimens of the *S. kralii* a priori group (82%) were assigned a posteriori to *S. kralii*; 6 specimens with 99-100% probability and 2 specimens with 74% and 70% probabilities. Two specimens of the *S. kralii* a priori group were assigned a posteriori to other species: 1 specimen to *S. arenicola* with 74% probability (*Semple & B. Semple 11208* WAT from Pulaski Co., Georgia) and 1 specimen to *S. racemosa* with 46% probability (44% to *S. kralii*; *Semple & B. Semple 11218* WAT from Aitken Co., South Carolina). Eight of 11 specimens of the *S. chlorolepsis* a priori group (73%) were assigned a posteriori to *S. chlorolepsis*; 6 specimens with 59-68% probability and 2 specimens with 49% probability (38% to *S. bellidifolia*: *Ringius 1702* WAT) and 48% probability (34% to *S. bellidifolia*; *Ringius 1800* WAT). Three specimens of the *S. chlorolepsis* a priori group were assigned a posteriori to other species: 2 specimens to *S. bellidifolia* with 65% probability (27% to *S. chlorolepis*: *Ringius 1702* WAT) and 26% probability (20% to *S. chlorolepis*, 18% to *S. ontarioensis*, 13% to *S. randii*, and 12% to *S. glutinosa*; *Dignard & Gagnon 98-69* QUE), and 1 specimen to *S. glutinosa* with 44% probability (20% to *S. chlorolepis*, 14% to *S. ontarioensis*, 11% to *S. bellidifolia*, and 10 to *S. randii*; *Ringius 1691c* WAT). All specimens of *S. chlorolepis* were from Mt. Albert and nearby peaks on the Gaspé,

Québec. Thirteen of 18 specimens of the *S. racemosa* a priori group (72%) were assigned a posteriori to *S. racemosa*; 9 specimens with 90-99% probability, 1 specimen with 86% probability, 2 specimens with 57% probability (*Semple & Ringius 7612* WAT from York Co., Pennsylvania; this was the most robust of the shoots collected from rocks above the Susquehana R.) and 56% probability (44% to *S. arenicola*; *Peirson 603* MICH from Nicholas Co., West Virginia), and 1 specimen with 36% probability (17% to *S. glutinosa*, 17% to S. randii, and 15% to S. simplex, *Dignard 99-114* QUE from Île-d'Anticosti, Québec). Five specimens of the *S. racemosa* a priori group were assigned a posteriori to other species: 1 specimen to *S. arenicola* with 90% probability (*Peirson 601* MICH from Barbour Co., West Virginia), 2 specimens to *S. randii* with 53% probability (*Labrecque s.n.* MT from Percé, Gaspésie, Québec) and 45% probability (*Semple & Keir 4621* WAT from Franklin Co., Maine), 1 specimen to *S. ontarioensis* with 50% probability (*Dignard et al. 08-95* QUE from Rivière Galiote, Île-d'Anticosti, Québec), and 1 specimen to *S. bellidifolia* with 24% probability (21% to *S. ontarionensis*, 17% to *S. randii*, 17% to *S. simplex*, and 13% to *S. glutinosa*; *Morton NA4142* TRT from Percé Mt., Gaspésie, Québec). Results for the remaining four species are summarized but not presented in detail. Six of 11 specimens of the *S. ontarioensis* a priori group (55%) were assigned a posteriori to *S. ontarioensis*; 1 specimen with 96% probability, 1 specimen with 86% probability, and 5 specimens with 50-30%. Five specimens of the *S. ontarioensis* a priori group were assigned a posteriori to other species: 1 specimen to *S. spathulata* with 100% probability, 1 specimen to *S. simplex* with 46% probability, 1 specimen to *S. bellidifolia* with 39% probability, 1 specimen to *S. randii* with 35% probability, and 1 specimen to *S. glutinosa* with 28% probability. Seven of 11 specimens of the *S. bellidifolia* a priori group (54%) were assigned a posteriori to *S. bellidifolia*; 1 specimen with 90% probability, 1 specimen with 85% probability, 2 specimens with 79% and 71% probabilities, 2 specimens with 59 and 52% probabilities, and 1 specimen with 36% probability. Six specimens of the *S. bellidifolia* a priori group were assigned a posteriori to *S. chlorolepis* with 54%, 54%, 50%, 39% and 37% probability. Eight of 15 specimens of the *S. randii* a priori group (53%) were assigned a posteriori to *S. randii*; 1 specimen with 75% probability, 1 specimen with 69% probability, and 4 specimens with 58%, 58%, 53% and 44% probability. Seven specimens of the *S. randii* a priori group were assigned a posteriori to other species: 1 specimen to *S. simplex* with 92% probability, 3 specimens to *S. glutinosa* with 75%, 28% and 21% probabilities, 1 specimen to *S. ontarioensis* with 39% probability, and 2 specimen to *S. chlorolepis* with 30% and 28% probabilities. Thirteen of 34 specimens of the *S. glutinosa* a priori group (38%) were assigned a posteriori to *S. glutinosa*; 1 specimen with 88% probability, 3 specimens with 72-75% probability, 2 specimens with 69% and 65% probabilities, 2 specimens with 58% and 52% probabilities, and 6 specimens with 43%, 41%, 40%, 37%, 36% and 32% probabilities. Twenty-one specimens of 34 the *S. glutinosa* a priori group were assigned a posteriori to other species: 9 specimens to *S. randii*, 4 specimens to *S.*

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*arenicola*	*bellidifolia*	*chlorolepis*	*gillmanii*	*glutinosa*	*kralii*	*ontarioensis*	*plumosa*	*racemosa*	*randii*	*simplex*	*spathulata*	% correct
arenicola	11	0	0	0	0	0	0	0	1	0	0	0	92
bellidifolia	0	7	6	0	0	0	0	0	0	0	0	0	54
chlorolepis	0	2	8	0	1	0	0	0	0	0	0	0	73
gillmanii	0	0	1	9	0	0	0	0	0	0	0	0	90
glutinosa	0	2	1	0	13	0	4	0	1	9	3	1	38
kralii	1	0	0	0	0	9	0	0	1	0	0	0	82
ontarioensis	0	1	0	0	1	0	6	0	0	1	1	1	55
plumosa	0	0	0	0	0	0	0	10	0	0	0	0	100
racemosa	1	1	0	0	0	0	1	0	13	2	0	0	72
randii	0	0	2	0	3	0	1	0	0	8	1	0	53
simplex	0	0	0	0	0	0	0	0	0	1	10	0	91
spathulata	0	0	0	0	1	0	0	0	0	0	1	0	83
TOTALS	13	13	18	9	19	9	12	10	16	21	16	10	68

Jackknifed classification matrix

Group	*areni-cola*	*bellidi-folia*	*chloro-lepis*	*gill-manii*	*glutin-osa*	*kralii*	*ontario-ensis*	*plum-osa*	*racem-osa*	*randii*	*simplex*	*spath-ulata*	% *correct*
arenicola	10	0	0	0	0	0	0	0	2	0	0	0	83
bellidifolia	0	6	7	0	0	0	0	0	0	0	0	0	46
chlorolepis	0	2	8	0	1	0	0	0	0	0	0	0	73
gillmanii	1	0	1	8	0	0	0	0	0	0	0	0	80
glutinosa	0	2	1	0	13	0	4	0	1	9	3	1	38
kralii	1	0	0	1	0	6	0	1	2	0	0	0	55
ontarioensis	0	1	0	1	1	0	5	0	0	1	1	1	45
plumosa	0	0	0	0	0	0	0	10	0	0	0	0	100
racemosa	1	1	0	0	0	0	1	0	13	2	0	0	72
randii	0	0	3	0	3	0	1	0	0	6	2	0	40
simplex	0	0	0	1	0	0	0	0	0	3	7	0	64
spathulata	0	0	0	0	1	0	0	0	0	0	1	10	83
TOTALS	13	12	20	11	19	6	11	11	18	21	14	12	61

ontarioensis, 2 specimens to *S. bellidifolia*, 1 specimen to *S. simplex,* and 1 specimen to *S. spathalata*. The specimen of *S. austrocaroliniana* was assigned a posteriori to *S. simplex* with 42% probability (19% to *S. racemosa*, 14% to *S. gillmanii*, 8% to *S. ontarioensis*, and 6% to *S. arenicola*.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 170 specimens including all species *Solidago* subsect. *Humiles* are presented in Fig. 25. Eigenvalues on the first three axes were 4.267, 2.229, and 1.308.

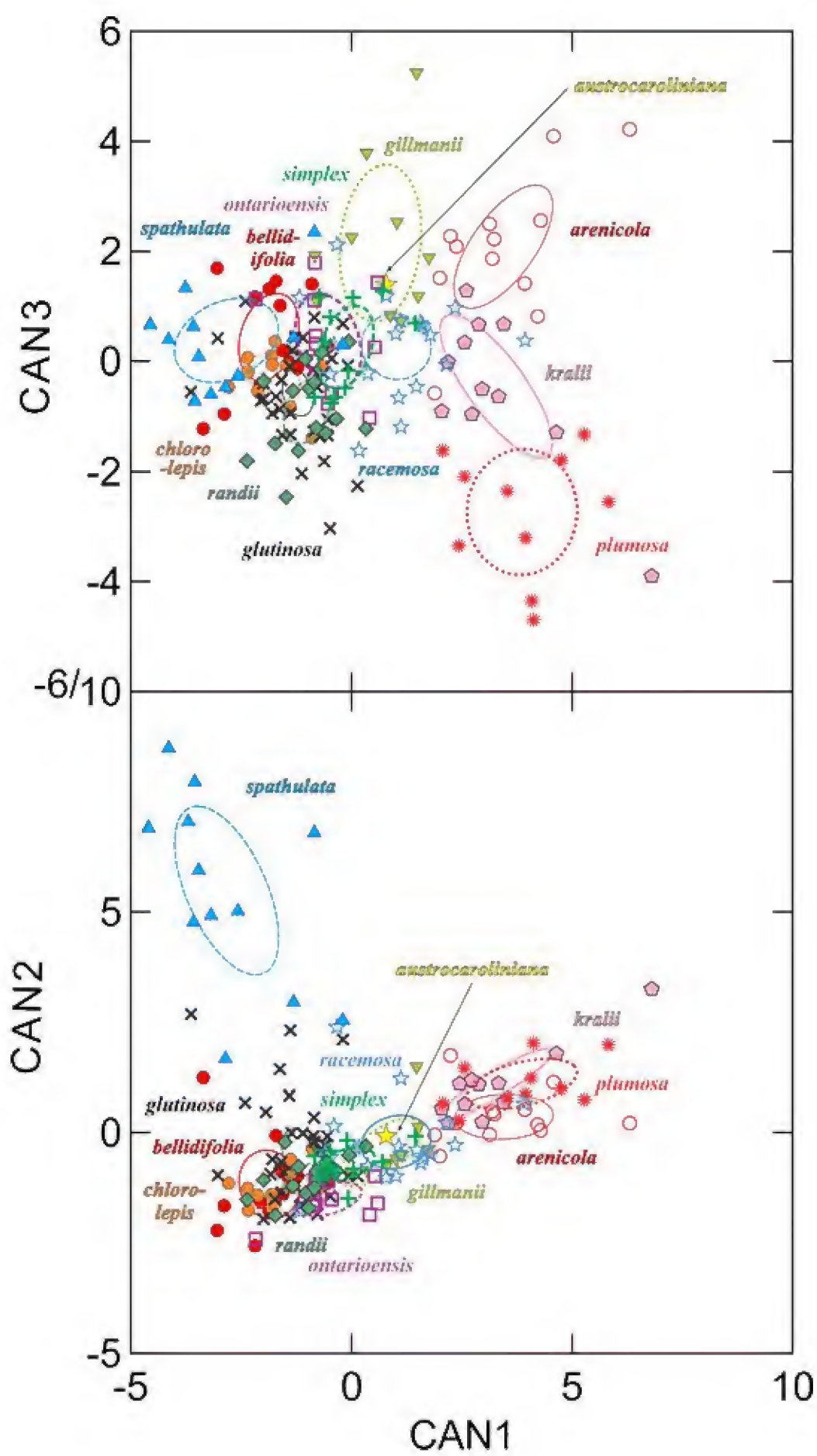

Figure 25. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 170 specimens of all species of *Solidago* subsect. *Humiles*: *S. austrocaroliniana* (yellow stars), *S. arenicola* (red circles), *S. bellidifolia* (red dots), *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black ×s), *S. kralii* (pink pentagons), *S. ontarioensis* (magenta squares), *S. plumosa* (red star-bursts), *S. racemosa* (open blue stars), *S. randii* (green diamonds), *S. simplex* (green +s), and *S. spathulata* (blue triangles).

Eleven species level a priori groups analysis

The Pearson correlation matrix for traits of specimens of *Solidago arenicola*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, and *S. simplex* included r > |0.7| for multiple pairs of leaf and floral traits. The following traits were included: stem height, mid stem leaf length, upper stem leaf width, number of upper stem leaf margin serrations, number of peduncle bracts, involucre height, mid series phyllary length, mid series phyllary width, number of ray florets, ray lamina length, number of disc florets, disc corolla lobe length, disc floret ovary/fruit body length, and disc floret pappus length at anthesis.

In the STEPWISE discriminant analysis of 156 specimens of eleven species level a priori groups (*Solidago arenicola*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, and *S. simplex*), the following eight traits were selected and are listed in order of decreasing F-to-remove values: stem height (14.76), number of peduncle bracts (11.08), number of ray florets (8.25), involucre height (7.70), upper stem leaf width (6.34), mid series phyllary width (6.07), mid stem leaf length (5.43), and disc floret pappus length at anthesis (4.44). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. bellidifolia* and *S. plumosa* (32.790); the smallest separations were between *S. glutinosa* and *S. randii* (2.006), between *S. glutinosa* and *S. ontarioensis* (2.450), between *S. randii* and *S. simplex* (2.808), and between *S. bellidifolia* and *S. chlorolepis* (2.904).

Table 4. Between groups F-matrix for the eleven a priori groups in a COMPLETE analysis (df = 8 138).

Group	*areni-cola*	*bellidi-folia*	*chloro-lepis*	*gill-manii*	*glutin-osa*	*kralii*	*ontario-ensis*	*plum-osa*	*racem-osa*	*randii*
bellidifolia	26.659									
chlorolepis	28.547	2.904								
gillmanii	12.786	13.220	11.935							
glutinosa	32.485	6.567	6.680	15.179						
kralii	12.437	30.760	30.676	15.161	27.935					
ontarioensis	17.337	4.593	4.488	9.555	2.450	22.555				
plumosa	16.160	32.790	28.292	25.247	33.174	12.256	24.159			
racemosa	10.679	10.620	10.715	11.653	12.414	18.167	6.178	16.825		
randii	28.510	5.907	3.611	13.471	2.006	22.947	3.704	26.540	9.285	
simplex	16.440	6.833	6.689	8.111	3.591	13.453	2.976	21.849	7.196	2.808

Wilks' lambda = 0.0120 df = 8 10 145; Approx. F= 11.1358 df = 80 883 prob = 0.0000

In the Classificatory Discriminant Analysis of 156 specimens of the twelve species level a priori groups (*Solidago arenicola*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, and *S. simplex*) plus 1 specimen of *S. austrocaroliniana* included a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 100-45%. The Classification matrix and Jackknife classification matrix are presented in Table 5. All 10 of the specimens of the *S. plumosa* a priori group were assigned a posteriori to *S. plumosa* with 9 specimens with 98-100% probability and 1 specimen with 88% probability. All 11 specimens of the *S. chlorolepis* a prior group were assigned a posteriori to *S. chlorolepis*: 1 specimen with 95% probability, 1 specimen with 80% probability, 1 specimen with 77% probability, 4 specimens with 65-66% probability, and 3 specimens with 52-48%. Eleven of the 12 specimens of the *S. arenicola* a priori group (92%) were assigned a posterior to the *S. arenicola*:

10 specimens with 94-100% probability and 1 specimen with 72% probability. One specimen of the *S. arenicola* a priori group was assigned a posteriori to *S. racemosa* with 38% probability (*Bailey B150* WAT from Scott Co., Tennessee). Twelve of the 13 specimens of the *S. bellidifolia* a priori group were assigned a posteriori to *S. bellidifolia*: 2 specimens with 96-97% probability, 3 specimens with 80-84% probability, 2 specimens with 75% and 70% probabilities, 2 specimens with 69% and 60% probabilities, and 3 specimens with 46% probability (*Ceska s.n.* V from Mt. Arrowsmith, Vancouver Is., British Columbia), 41% probability (*Semple & Xiang 10270* WAT from Mt. Hood, Oregon), and 32% probability (*Semple & Xiang 10270* WAT from Mt. Hood, Oregon). Nine of the 10 specimens of the *S. gillmanii* a priori group specimens (90%) were assigned a posteriori to *S. gillmanii*: 7 specimens with 90-100% probability, 1 specimen with 88% probability, and 1 specimen with 57% probability. One specimen of the *S. gillmanii* a priori group was assigned a posteriori to *S. chlorolepsis* with 41% probability (*Ringius 1851* WAT from Door Co., Wisconsin). Nine of the 11 specimens of the *S. kralii* a priori group (82%) were assigned to the *S. kralii* a priori group: 7 specimens with 99-100% probability, 1 specimen with 87% probability, and 1 specimen with 69% probability. Two specimens of the the *S. kralii* a priori group were assigned to other species: 1 specimen to *S. arenicola* with 69% probability (*Semple & B. Semple 11208* WAT from Pulaski Co., Georgia) and 1 specimen to *S. racemosa* with 52% (*Semple & B. Semple 11218* WAT from Aiken Co., South Carolina). Nine of the 11 specimens of the *S. simplex* a priori group (82%) were assigned a posteriori to the *S. simplex* a priori group: 1 specimen with 93% probability, 2 specimens with 89% and 86% probabilities, 5 specimens with 51-59% probability, and 1 specimen with 33% probability. Two specimens of the *S. simplex* a priori group were assigned to *S. randii* with 38% and 28% probabilities. Thirteen of the 18 specimens of the *S. racemosa* a priori group (72%) were assigned a posteriori to *S. racemosa*: 8 specimens with 93-99% probability, 3 specimens with 83-85% probability, 1 specimen with 62% probability, and 1 specimen with 29% probability. Five specimens of the *S. racemosa* a priori group were assigned to other species: 1 specimen to *S. arenicola* with 86%, 2 specimens to *S. randii* with 51% and 38% probabilities, and 2 specimens to *S. ontarioensis* with 47% and 25% probabilities. For the other three species percents of correct assignment to the a priori species were much lower. Seventeen of the 34 specimens of the *S. glutinosa* a priori group (50%) were assigned a posteriori to *S. glutinosa*: 1 specimen with 82% probability, 2 specimens with 76% and 72% probabilities, 4 specimens with 61-69% probability, and 10 specimens with 54-33% probability. Seventeen specimens of the *S. glutinosa* a priori group were assigned a posteriori to 5 other species. Seven of the 15 specimens of the *S. randii* a priori group (47%) were assigned a posteriori to *S. randii*: 2 specimens with 83-84% probability, 1 specimen with 70% probability, 1 specimen with 61% probability, and 3 specimens with 57-45% probability. Eight specimens of the *S. randii* a priori group were assigned a posteriori to other species: 4 specimens to *S. chlorolepis* with 53-38% probability, 3 specimens to *S. glutinosa* with 68-39% probability, and 1 to *S. simplex* with 90% probability. Five of the 11 specimens of the *S. ontarioensis* a priori group (45%) were assigned a posteriori to *S. ontarioensis*: 2 specimens with 98-96% probability and 3 specimens with 53-40% probability. Six specimens of the *S. ontarioensis* a priori group were assigned a posteriori to other species: 3 specimens to *S. glutinosa* with 66-35% probability, 1 specimen to *S. bellidifolia* with 68% probability, 1 specimen to *S. simplex* with 41% probability, and 1 specimen to *S. gillmanii* with 34% probability. The 1 specimen of *S. austrocaroliniana* included a posteriori was assigned to to *S. simplex* with 36% probability (27% to *S. gillmanii*, 20% to *S. racemosa*, and 7% to *S. ontarioensis*).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 158 specimens of all species of *S.* subsect. *Humiles* are presented in Fig. 26. Eigenvalues on the first three axes were 4.603, 1.384, and 1.110.

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*areni-cola*	*bellidi-folia*	*chloro-lepis*	*gill-manii*	*glutin-osa*	*kralii*	*ontario-ensis*	*plum-osa*	*racem-osa*	*randii*	*simplex*	% correct
arenicola	11	0	0	0	0	0	0	0	1	0	0	92
bellidifolia	0	12	1	0	0	0	0	0	0	0	0	92
chlorolepis	0	0	11	0	0	0	0	0	0	0	0	100
gillmanii	0	0	1	9	0	0	0	0	0	0	0	90
glutinosa	0	3	0	0	17	0	5	0	1	7	1	50
kralii	1	0	0	0	0	9	0	0	1	0	0	82
ontarioensis	0	1	0	1	3	0	5	0	0	0	1	45
plumosa	0	0	0	0	0	0	0	10	0	0	0	100
racemosa	1	0	0	0	0	0	2	0	13	2	0	72
randii	0	0	4	0	3	0	0	0	0	7	1	47
simplex	0	0	0	0	0	0	0	0	0	2	9	82
TOTALS	13	16	17	10	23	9	12	10	16	18	12	72

Jackknifed classification matrix

Group	*areni-cola*	*bellidi-folia*	*chloro-lepis*	*gill-manii*	*glutin-osa*	*kralii*	*ontario-ensis*	*plum-osa*	*racem-osa*	*randii*	*simplex*	% correct
arenicola	11	0	0	0	0	0	0	0	1	0	0	92
bellidifolia	0	11	1	0	0	0	0	0	0	1	0	85
chlorolepis	0	1	10	0	0	0	0	0	0	0	0	91
gillmanii	1	0	1	8	0	0	0	0	0	0	0	80
glutinosa	0	4	1	0	16	0	4	0	1	7	1	47
kralii	1	0	0	0	0	8	0	1	1	0	0	73
ontarioensis	0	1	0	1	4	0	3	0	0	0	2	27
plumosa	0	0	0	0	0	0	0	10	0	0	0	100
racemosa	1	0	0	0	0	0	2	0	12	2	1	67
randii	0	0	4	0	3	0	0	0	0	6	2	40
simplex	0	0	0	0	0	0	1	0	1	2	7	64
TOTALS	14	17	17	9	23	8	10	11	16	18	13	65

Four western species level a priori groups analysis

The Pearson correlation matrix for traits of specimens of *Solidago bellidifolia*, *S. glutinosa*, *S. simplex* and *S. spathulata* included r > |0.7| for most pairs of leaf traits reducing those included to mid stem leaf width, upper stem leaf length and number of margin serrations, the number of upper stem nodes in the top 25% below the inflorescence, and the number of peduncle bracts. Basal rosette leaves were often not present and were not included in the discriminant analyses. Many floral traits were correlated, and only involucre height, the numbers of rays, ray floret lamina length and width, number of disc florets, the lengths of disc corolla and corolla lobes, fruit/ovary body, and pappus were included in the STEPWISE analysis.

In the STEPWISE discriminant analysis of 67 specimens of four species level a priori groups in (*Solidago bellidifolia*, *S. glutinosa*, *S. simplex,* and *S. spathulata*), the following four traits were selected and are listed in order of decreasing F-to-remove values: number of upper leaf margin serrations (50.21), upper stem leaf length (22.57), number of ray florets (10.78), and number of disc florets (7.65). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. glutinosa* and *S. spathulata* (46.606); the smallest separation was between *S. glutinosa* and *S. simplex* (8.389).

In the Classificatory Discriminant Analysis of 67 specimens of the four species level a priori groups (*S. bellidifolia*, *S. glutinosa*, *S. simplex*, and *S. spathulata*) plus 3 specimens included a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 82-100%.

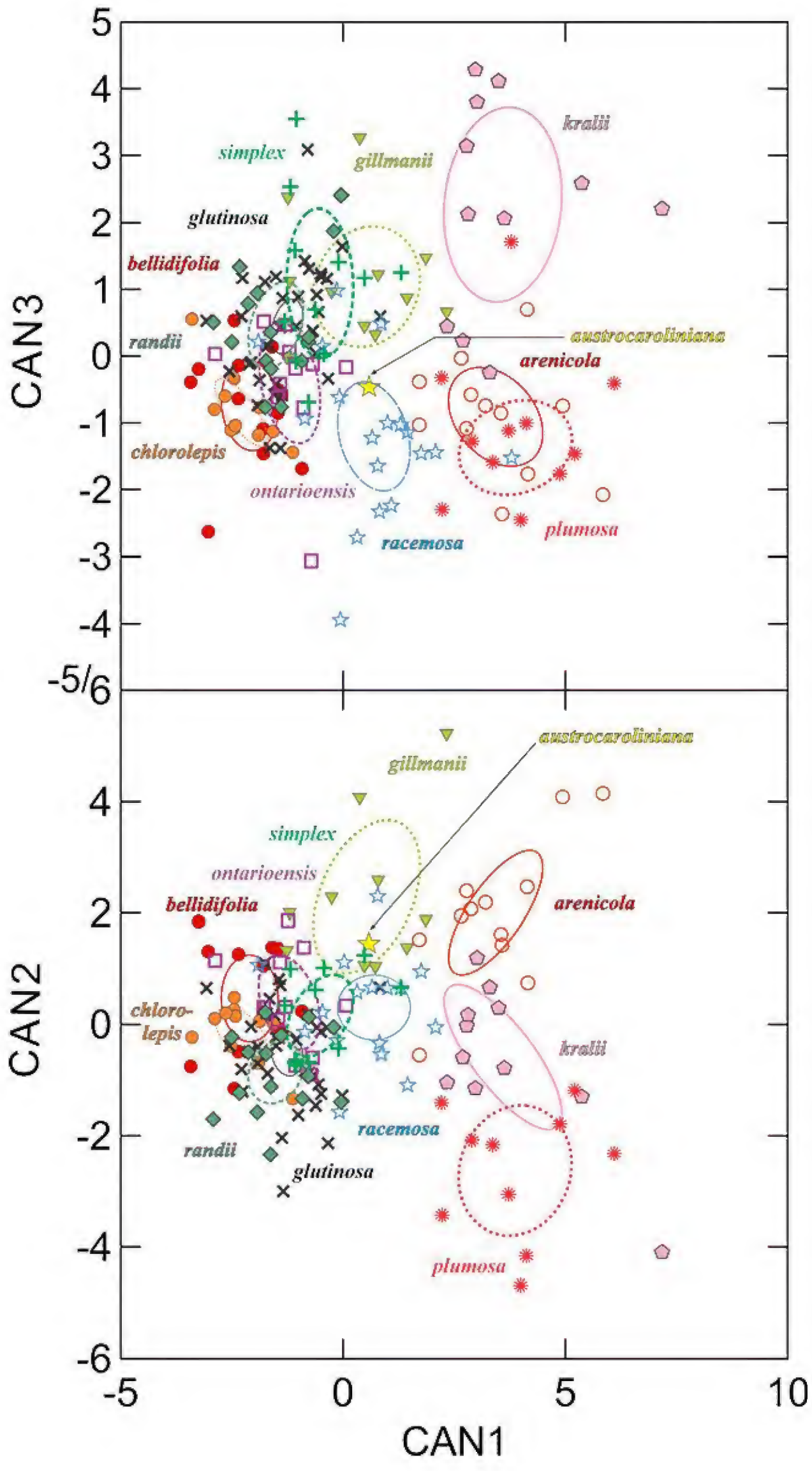

Figure 26. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 158 specimens of *Solidago* subsect. *Humiles*: *S. austrocaroliniana* (yellow stars), *S. arenicola* (red circles), *S. bellidifolia* (red dots), *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black ×s), *S. kralii* (pink pentagons), *S. ontarioensis* (magenta squares), *S. plumosa* (red star-bursts), *S. racemosa* (open blue stars), *S. randii* (green diamonds), and *S. simplex* (green +s).

Table 6. Between groups F-matrix for the four species level a priori groups analysis (df = 4 60).

Group	*bellidifolia*	*glutinosa*	*simplex*
glutinosa	13.525		
simplex	13.907	8.389	
spathulata	30.057	46.606	36.388

Wilks' lambda = 0.0781 df = 4 3 63; Approx. F= 21.4788 df = 12 159 prob = 0.0000

The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 13 specimens of *S. bellidifolia* a priori group (100%) were assigned a posteriori into the *S. bellidifolia* group; 9 specimens with 90-100% probability 2 specimens with 83% and 81% probability, 1 specimen with 62% probability, and 1 specimen with 56% probability (43% to *S. glutinosa*; *Ceska s.n.* from Forbidden Plateau, Vancouver Is., British Columbia). Nine of 11 specimens of the *S. spathulata* a priori group (82%) plus 1 additional specimen included a posteriori were assigned a posteriori to *S. spathulata* with 95-100% probability. Two specimens of the *S. spathulata* a priori group were assigned to *S. bellidifolia* with 82% probability (13% to *S. spathulata; Semple & Heard 8541* WAT from Mendocino Co., California) and 66% probability (18% to *S. spathulata* and 15% to *S. glutinosa*; *J.K. Morton NA3312* TRT from Lincoln Co., Oregon, coastal dunes). Twenty-six of 32 specimens of the *S. glutinosa* a priori group (82%) were assigned a posteriori into the *S. glutinosa* group; 8 specimen with 91-99% probability, 2 specimens with 89% and 80% probabilities, 6 specimens with 70-75% probability, 6 species with 60-68% probability, and 2 specimens with 55% probability (37% to *S. simplex*; *Morton & Venn NA14135* TRT from Muncho Lake Prov. Park, British Columbia) and 53% probability (40% to *S. glutinosa*; *Semple & Heard 7747* WAT from Gunnison Co., Colorado; dwarf shoots 10-14 cm tall). Six specimens of the *S. glutinosa* a priori group plus 1 additional specimen included a posteriori were assigned to other species: 1 specimen to S. *spathulata* with 93% probability (*Zika 22787* WTU from Thurston Co., Washington; small shoots from rocky prairie, 70 m ele.); 3 specimens to *S. bellidifoia* with 67% probability (46% to *S. glutinosa; Russell 66-129* WAT from Pitkin Co., Colorado), 55% probability (40% to *S. glutinosa*; *Semple & B. Semple 11239* WAT from Summit Co., Colorado), and 54% probability (46% to *S. glutinosa*; *Morton NA2095* TRT from Mt. Fairplay, Alaska), and 3 specimens to *S. simplex* with 78% probability (21% to *S. glutinosa; Montague & Montague 35* WTU from Thurston Co., Washington; open prairie, 50 m ele.), 58% probability (42% *S. glutinosa*; *Semple & B. Semple 6548* WAT from Boulder Co., Colorado), and 50% probability (53% to *S. glutinosa*; *Ringius 1978* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 18 cm tall shoot). Eight of 10 specimens of the *S. simplex* a priori group (82%) plus 1 specimen included a posterior were assigned a posteriori to the *S. simplex* group: 5 specimens with 94-100% probability and 3 specimens with 83-89% probability. Two specimens of the *S. simplex* a priori group plus 1 specimen included a posteriori were assigned a posteriori to other species: 2 specimens to *S. glutinosa* with 68% probability (29% to *S. simplex; Pringle 10294* GH from Esdo. Hidalgo, Mexico) and 40% probability (31% to *S. simplex* and 29% to *S. bellidifolia; Hinton et al. 22298* TEX from Esdo. Nuevo Leon, Mexico); and 1 specimen to *S. bellidifolia* with 61% probability (29% to *S. glutinosa; Roe et al. 247* LL from Esdo. Hidalgo, Mexico).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 69 specimens of *Solidago bellidifolia*, *S. glutinosa*, *S. simplex*, and *S. spathulata* are presented in Fig. 27. Eigenvalues on the first two axes were 3.354 and 0.919.

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*bellidifolia*	*glutinosa*	*simplex*	*spathulata*	% correct
bellidifolia	13	0	0	0	100
glutinosa	3	26	2	1	81
simplex	1	2	8	0	73
spathulata	2	0	0	9	82
Totals	19	28	10	10	84

Jackknifed classification matrix

Group	*bellidifolia*	*glutinosa*	*simplex*	*spathulata*	% correct
bellidifolia	12	1	0	0	92
glutinosa	4	25	2	1	78
simplex	1	2	8	0	73
spathulata	2	0	0	9	82
Totals	19	28	10	10	81

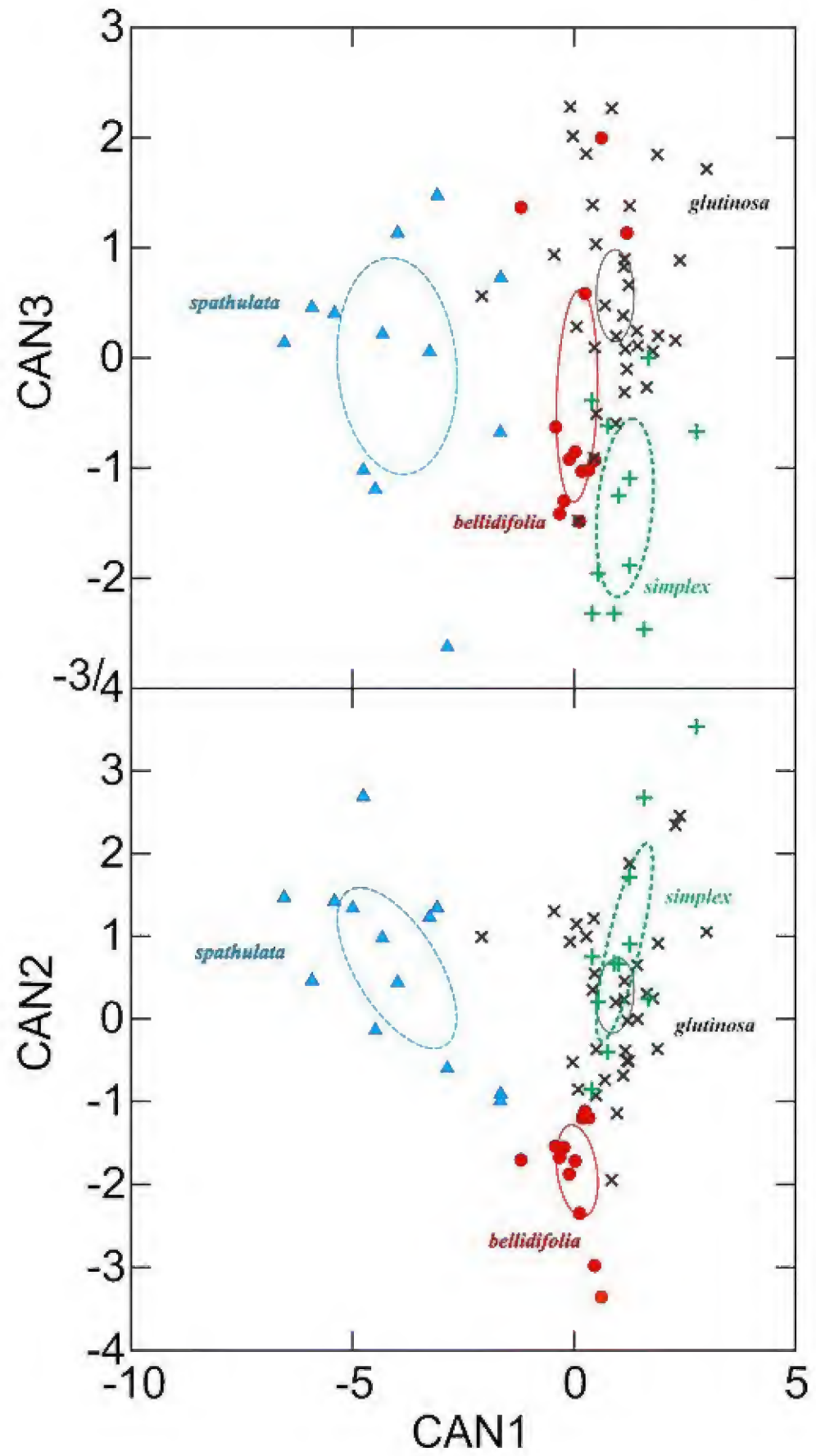

Figure 27. Plot of canonical scores (CAN1 vs CAN2) analysis for 69 specimens of *Solidago* subsect. *Humiles*: *S. bellidifolia* (red dots), *S. glutinosa* (black ×s), *S. simplex* (green +s), and *S. spathulata* (blue triangles).

Two species level a priori groups analysis: Solidago bellidifolia and S. glutinosa

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length, width and number of serrations. Most floral traits were not highly correlated. Involucre height correlated with mid series phyllary length; the latter was excluded from the analysis. Ray floret fruit body and pappus lengths correlated with disc floret fruit body length and disc floret corolla length, respectively; the disc floret traits were included in the analysis.

In the STEPWISE discriminant analysis of 45 specimens of two species level a priori groups (*S. bellidifolia* and *S. glutinosa*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid leaf length (40.61), ray floret lamina width (9.82), and involucre height (6.22). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago bellidifolia* and *S. glutinosa* had an F-to separate value of 19.607 (Wilks' lambda = 0.4107 df = 3 1 43; Approx. F= 19.6066 df = 3 41 prob = 0.0000).

In the Classificatory Discriminant Analysis of 45 specimens of the two species level a priori groups (*S. bellidifolia* and *S. glutinosa*), percents of correct a posterori assignment to the same a priori group were 100% and 87%. The Classification matrix and Jackknife classification matrix are presented in Table 8. All 14 specimens of the *S. bellidifolia* a priori group (100%) were assigned a posteriori into the *S. bellidifolia* group; 10 specimens with 90-100% probability, 3 specimens with 83-89% probability, and 1 specimen with 76% probability. Twenty-seven of 31 specimens of the *S. glutinosa* a priori group (93%) were assigned a posteriori into the *S. glutinosa* group; 20 specimens with 90-100% probability, 2 specimens with 88-89% probability, 2 specimens with 77% and 75% probabilities, and 2 specimens with 60% probability each. Four specimens of the *S. glutinosa* a priori group were assigned to *S. bellidifolia* with 56% probability (*Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 19 cm tall shoot), 56% probability (*Semple & Xiang 102011* WAT from Johnston Co., Wyoming; small shoot 25 cm tall), 54% probability (83 *Semple & Heard 7747* WAT from Gunnison Co., Colorado; dwarf shoots 10-14 cm tall) and 51% probability (*Semple & Heard 7827* WAT from Beaver co., Utah; dwarf shoots 15-17 cm tall).

Frequencies of CAN1 canonical scores for 45 specimens of *S. bellidifolia* and *S. glutinosa* are presented in histograms in Fig. 28. The Eigenvalue on the first axis was 1.435.

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two a priori groups (*S. glutinosa* and *S. glutinosa*); a posteriori placement to groups in rows.

Group	***bellidifolia***	***glutinosa***	**% correct**
bellidifolia	14	0	100
glutinosa	4	27	87
Totals	18	27	91

Jackknifed classification matrix

Group	***bellidifolia***	***glutinosa***	**% correct**
bellidifolia	14	0	100
glutinosa	4	27	87
Totals	18	27	91

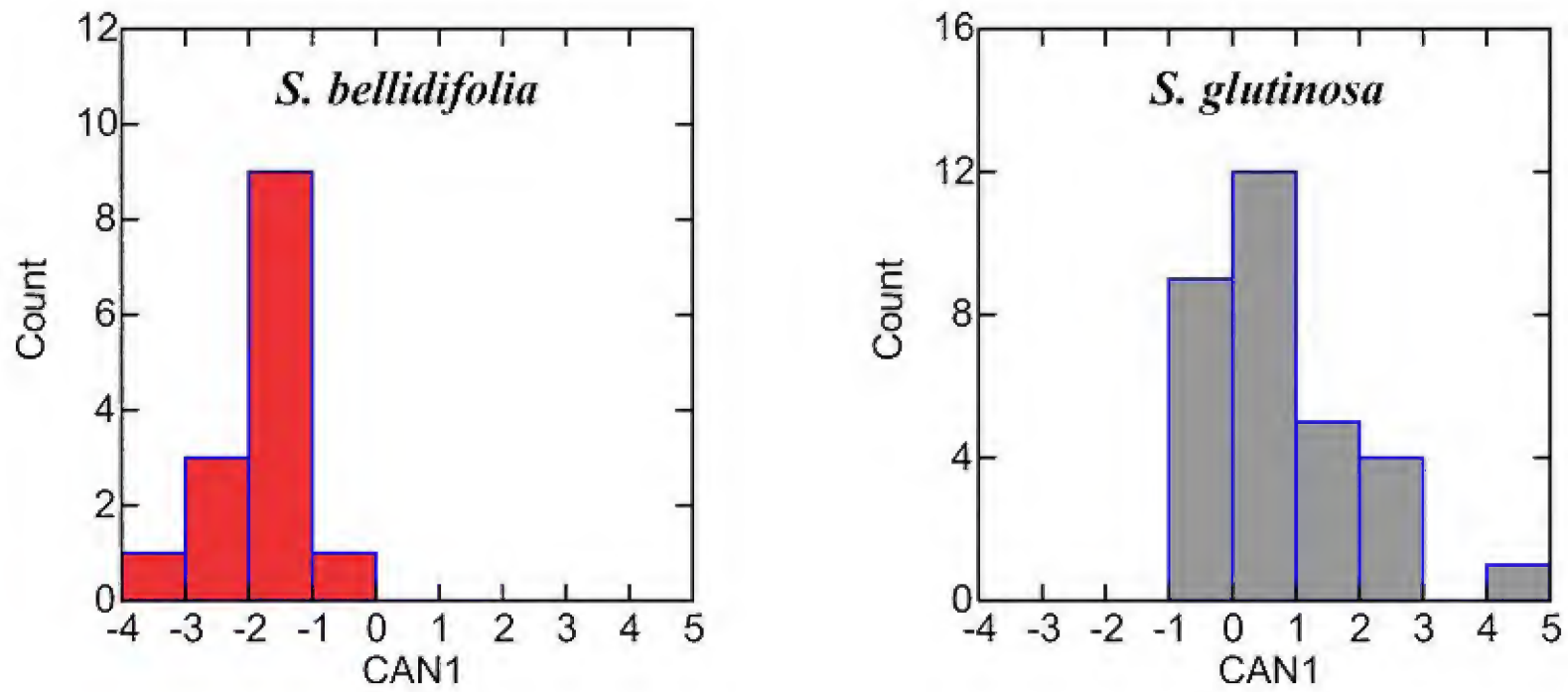

Figure 28. Histograms of CAN1 canonical scores for 45 specimens of *S. bellidifolia* (left) and *S. glutinosa* (right).

Two species level a priori groups analysis: Solidago glutinosa and S. simplex

The Pearson correlation matrix yielded r > |0.7| for multiple pairs of leaf traits and floral traits. The following traits were included in the analysis: mid stem leaf length and numbers of margin serrations, upper stem leaf width and number of margin serrations, number of peduncle bracts, involucre height, mid series phyllary width, number of ray florets, ray floret lamina length and width, and number of disc florets, disc floret lobe, ovary/fruit body, and pappus lengths.

In the STEPWISE discriminant analysis of 44 specimens of two species level a priori groups (*S. glutinosa* and *S. simplex*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (29.71), number of ray florets (22.91, and upper stem leaf width (7.23), Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago glutinosa* and *S. simplex* had an F-to separate value of 16.245 (Wilks' lambda = 0.451 df = 14 1 42; Approx. F= 16.245 df = 4 40 prob = 0.0000).

In the Classificatory Discriminant Analysis of 44 specimens of the two species level a priori groups (*S. glutinosa* and *S. simplex*), percents of correct a posterori assignment to the same a priori group were 97% and 91% respectively. The Classification matrix and Jackknife classification matrix are presented in Table 9. Thirty-two of the 33 specimens of the *S. glutinosa* a priori group (97%) were assigned a posteriori into the *S. glutinosa* group; 21 specimens with 90-100% probability, 3 specimens with 83-89% probability, 3 specimens with 73-77% probability, 1 specimen with 66% probability, and 4 specimens with 59% probability (*Semple & B. Semple 6548* WAT from Boulder Co., Colorado), 57% probability (*Semple & B Semple 5511* WAT from Mineral Co., Colorado), 53% probability (*Russell 66-129* WAT from Pitkin Co., Colorado), and 53% probability (*Hammond 10804* DES from San Pedro Martir Mts., Baha California, Mexico). One specimen of the *S. glutinosa* a priori group was assigned a posteriori to *S. simplex* with 77% probability (*Montague & Montague 35* WTU from Thurston Co., Washington). Ten of the 11 specimens of the *S. simplex* a priori group (91%) were assigned a posteriori into *S. simplex*: 7 specimens with 90-100% probability, 1 specimen with 87% probability, 1 specimen with 74% probability, and 1 specimen with 56% probability (*Hinton et al. 22298* TEX Esdo. Nuevo Leon, Mexico). One specimen of the *S. simplex* a priori group was assigned to *S. glutinosa* with 94% probability (*Roe et al. 247* LL from Esdo. Hidalgo, Mexico).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	*glutinosa*	*simplex*	% correct
glutinosa	32	1	97
simplex	1	10	91
Totals	33	11	95

Jackknifed classification matrix

Group	*glutinosa*	*simplex*	% correct
glutinosa	30	3	91
simplex	1	10	91
Totals	31	13	91

Frequencies of CAN1 canonical scores for 48 specimens of *S. glutinosa* and *S. simplex* are presented in histograms in Fig. 29. The Eigenvalue on the first axis was 1.564.

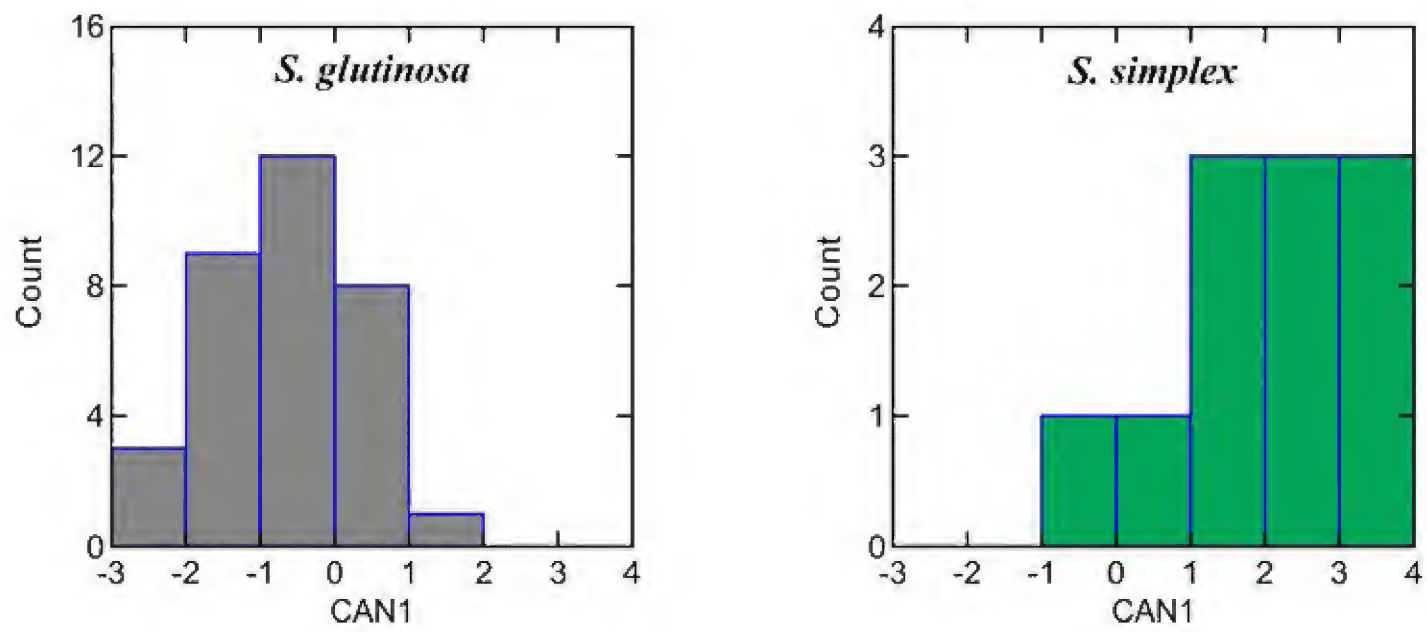

Figure 29. Histograms of CAN1 canonical scores for 44 specimens of *S. glutinosa* (left) and *S. simplex* (right).

Six northeastern species level a priori groups analysis 1

The Pearson correlation matrix yielded r > |0.7| for multiple pairs of leaf traits reducing the number to be used to lower stem leaf length and number of margin serrations, mid stem leaf width, and upper stem leaf length. Involucre height correlated with mid series phyllary length and disc floret corolla length; the first trait was included in the analysis. Ray floret ovary/fruit traits correlated with disc floret ovary/fruit traits; ray floret pappus length and disc floret ovary/fruit body length were included in the analysis.

In the STEPWISE discriminant analysis of 94 specimens of six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*), the following eight traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (17.25), upper stem leaf length (12.93), mid series phyllary width (10.20), ray floret pappus length at anthesis (8.06), involucre height (7.76), mid stem leaf width (4.98), number of ray florets (4.66), and disc floret ovary/fruit body length (4.45). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had

probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 10. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. chlorolepis* and *S. glutinosa* (22.481); the smallest separation was between *S. chlorolepis* and *S. randii* (4.049).

Table 10. Between groups F-matrix for the six a priori groups of northeastern taxa (df = 8 81).

Group	*chlorolepis*	*gillmanii*	*glutinosa*	*ontarioensis*	*racemosa*
gillmanii	16.553				
glutinosa	11.538	22.481			
ontarioensis	7.556	10.516	5.696		
racemosa	11.319	12.082	14.537	5.058	
randii	4.049	19.478	6.340	8.406	11.382

Wilks' lambda = 0.0362 df = 8 5 88; Approx. F= 10.1288 df = 40 355 prob = 0.0000

In the Classificatory Discriminant Analysis of 94 specimens of the six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii*) plus 4 additional specimens included a posteriori, were assigned a posterori to the same a priori group with percents correct of 75-100%. The Classification matrix and Jackknife classification matrix are presented in Table 11. All 11 of the specimens of the *S. chlorolepis* a priori group (100%) assigned a posteriori into the *S. chlorolepis* group; 6 specimens with 92-100% probability, 3 specimens with 87-89% probability, and 2 specimens with 56% probability (*Ringius 1691* WAT from Mt. Albert, Gaspé, Québec) and 50% probability (*Dignard & Gagnon 98-69* QUE from a peak WSE of Mt. Albert). Thirteen of the 14 specimens of the *S. randii* a priori group (93%) were assigned a posteriori to the *S. randii* group; 5 specimens with 95-100% probability, 2 specimens with 89% probability, 3 specimens with 60-66% probability, and 3 specimens with 51% probability and 42% probability (*Ringius 1759* WAT and *Ringius 1760b* WAT from Cadillac Mt. on Mount Desert Is., Maine), and 37% probability (*Ringius 1807a* WAT from Thetford Mines, Québec). One specimen of the *S. randii* a priori group plus 1 additional specimen included a posteriori were assigned a posteriori to *S. glutinosa* with 93% probability (*Beaudry 58-246* NY from Smuggler's Notch, Lamoille Co., Vermont) and 43% probability (*Ferguson & Attley s.n.* NY from Bald Mt., Fulton Chain, Herkimer Co., New York). Nine of the 10 specimens of *S. gillmanii* a priori group (90%) were assigned a posteriori to the *S. gillmanii* group with 98-100% probability. One specimen of the *S. gillmanii* a priori group was assigned to *S. chlorolepis* with 55% probability (35% to *S. gillmanii*; *Ringius 1851* WAT from Door Co., Wisconsin). Nine of the 11 specimens of the *S. ontarioensis* a priori group (82%) plus 1 additional specimen included a posteriori were assigned a posteriori to the *S. ontarioensis* group; 4 specimens with 92-100% probability, 2 specimens with 78% and 76% probabilities, 1 specimen with 61% probability, and 2 specimens with 57% probability (*Semple & Brammall 2787* WAT from Tobermory, Bruce Co., Ontario) and 53% probability (*Semple & Brammall 2788* WAT from E of Tobermory, Bruce Co., Ontario). Two specimens of the *S. ontarioensis* a priori group were assigned a posteriori to other species: 1 specimen to *S. glutinosa* with 69% probability (*Morton NA3691* TRT from Tobermory, Bruce Co., Ontario) and 1 specimen to *S. randii* with 65% probability (*Morton & Venn NA7620* TRT from Flower Pot Is., Bruce Co., Ontario). Twenty-six of the 32 specimens of the *S. glutinosa* a priori group (81%) were assigned a posteriori to the *S. glutinosa* group; 14 specimens with 91-99% probability, 2 specimens with 85% and 81% probability, 3 specimens with 72-78% probability, 4 specimens with 61-68% probability, and 2 specimens with 49% probability (48% to *S. simplex*; *Semple & B. Semple 6556* WAT from Summit Co., Colorado) and 46% probability (*Semple & Brouillet 4283* WAT from W of Mannville, Albert). Six specimens of the *S. glutinosa* a priori

group plus 2 additional specimens included a posteriori were assigned a posteriori to other species: 3 specimens to *S. randii* with 91% probability (*Semple & Semple 11239* WAT from 10,400' ele., Summit Co., Colorado), 78% probability (*Morton NA1854* TRT from Bordon, Saskatchewan), 48% probability (47% to *S. glutinosa*; *Peirson 647* WAT from Otsego Co., Michigan; involucres were on average 3.5 mm high; Peirson et al. 2012 reported the population to be diploid), and 37% probability (33% to *S. glutinosa*; *Peirson 466* WAT from Presque Isle Co., Michigan; 63 cm tall shoot); 2 specimens to *S. ontarioensis* with 70% probability (22% to *S. glutinosa*; *Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 19 cm tall shoot) and 52% probability (29% to *S. glutinosa*; *Hammond 10804* DES from San Pedro Martir Mts., Baha California, Mexico); 1 specimen to *S. racemosa* with 94% probability (*Pavlick 80-431* V from 51° 55' N 122° 20' W, British Columbia; Fig. 7; robust plant); and 1 specimen to *S. chlorolepis* with 55% probability (31% to *S. simplex* and 12% to *S. glutinosa*; *Russell 66-129* WAT from 11000' ele, Independence Pass, Colorado; dwarf shoots 7-11 cm tall). Twelve of the 16 specimens of the *S. racemosa* a priori group (75%) plus 1 additional specimen included a posteriori were assigned a posteriori to the *S. racemosa* group; 10 specimens with 95-100% probability, 2 specimens with 63% probability and 62% probability, and 1 specimen with 52% probability (32% to *S. randii*; *Semple & Keir 4621* WAT from Franklin Co., Maine). Four specimens of the *S. racemosa* a priori group were assigned a posteriori to other species: 3 specimens to *S. ontarioensis* with 86% probability (*Labrecque s.n.* MT from Percé, Gaspésie, Québec), 77% probability (*Morton NA4142* TRT from Percé Mt., Gaspésie, Québec), and 70% probability (*Semple & Ringius 7612* WAT from York Co., Pennsylvania); and 1 specimen to *S. randii* with 31% probability (22% to *S. ontarioensis*, 19% to *S. racemosa*, 18% to *S. chlorolepis*, and 10% to *S. glutinosa*; *Dignard et al. 08-95* QUE from Île-d'Anticosti, Québec).

Table 11. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six species level a priori groups; a posteriori placements to groups in rows.

Group	*chlorolepis*	*gillmanii*	*glutinosa*	*ontarioensis*	*racemosa*	*randii*	% correct
chlorolepis	11	0	0	0	0	0	100
gillmanii	1	9	0	0	0	0	90
glutinosa	1	0	26	1	1	3	81
ontarioensis	0	0	1	9	0	1	82
racemosa	0	0	0	3	12	1	75
randii	0	0	1	0	0	13	93
Totals	13	9	28	13	13	18	85

Jackknifed classification matrix

Group	*chlorolepis*	*gillmanii*	*glutinosa*	*ontarioensis*	*racemosa*	*randii*	% correct
chlorolepis	10	0	0	0	0	1	91
gillmanii	1	9	0	0	0	0	90
glutinosa	1	0	23	2	1	4	72
ontarioensis	1	1	3	4	1	1	36
racemosa	0	1	0	3	10	2	63
randii	1	0	3	0	0	6	71
Totals	14	11	29	9	12	14	70

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 97 specimens of *Solidago chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii* are presented in Fig. 30. Eigenvalues on the first three axes were 2.699, 1.293, and 0.961.

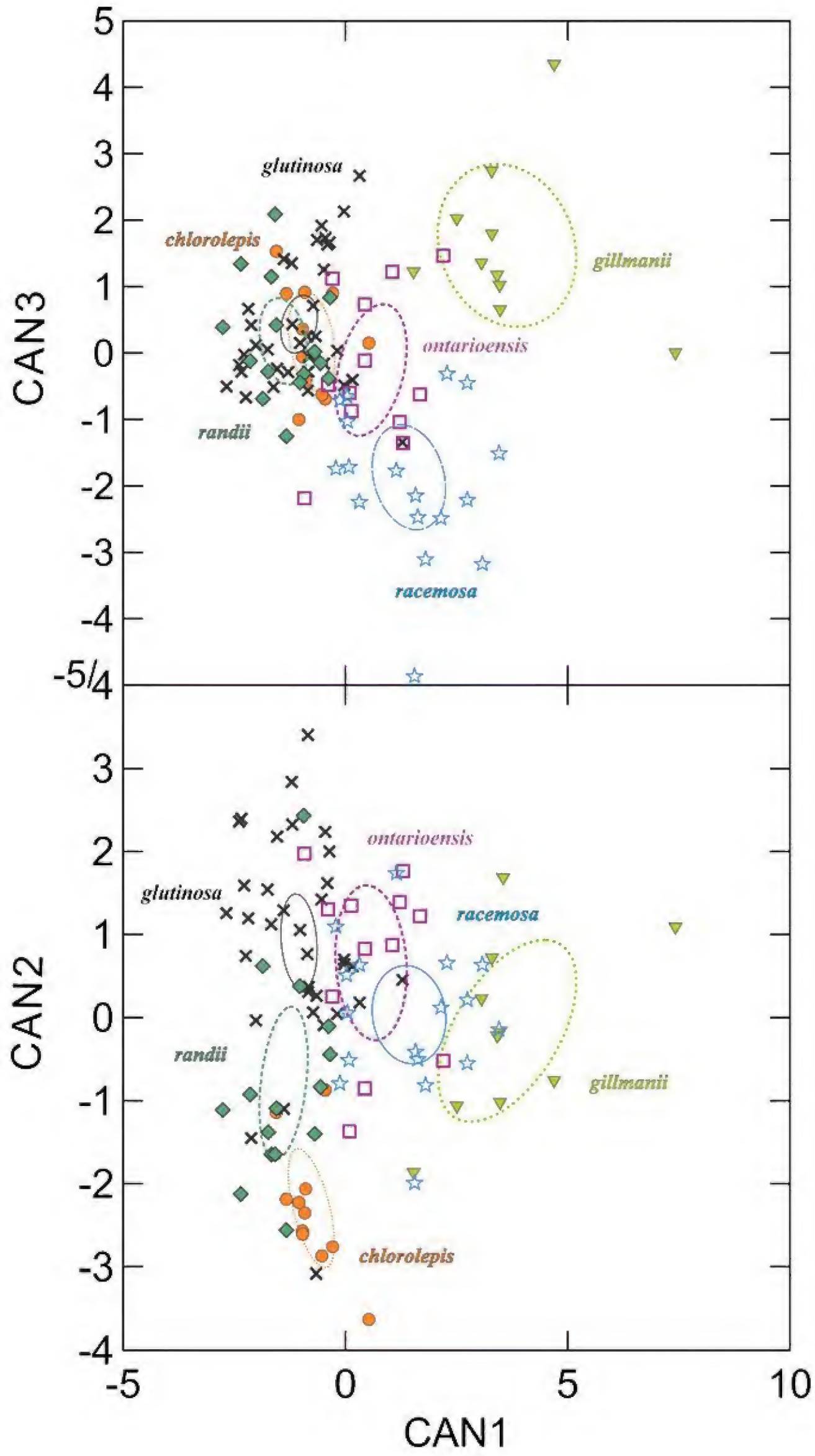

Figure 30. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) from the STEPWISE analysis of 94 specimens plus 3 additional ones a posteriori northeastern species of *Solidago* subsect. *Humiles*: *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black ×s), *S. ontarioensis* (magenta squares), *S. racemosa* (open blue stars), and *S. randii* (green diamonds).

Six northeastern species level a priori groups analysis 2

In order to determine how a large number of traits could be utilized to separate the six northeastern species into groups, a COMPLETE analysis was run using the following 21 traits ignoring the amount of correlation between traits: stem height, lower stem leaf length, width, and number of margin serrations, mid stem leaf length, width, and number of margin serrations, upper stem leaf length, width, and number of margin serrations, number of peduncle bracts, involucre height, mid series phyllary length, number of ray florets, ray floret lamina length and width, number of disc florets, disc corolla length and lobe length, disc floret ovary/immature fruit body length, and disc floret pappus length at anthesis.

In the COMPLETE discriminant analysis of 94 specimens of six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*), the following 8 traits had the highest F-to-removes values and are listed in order of decreasing F-to-remove values: stem height (9.65), disc floret pappus length at anthesis (4.82), involucre height (3.91), number of ray florets (3.91), number of peduncle bracts (3.43), number of upper stem leaf margin serrations (3.17), mid stem leaf width (2.92), and lower stem leaf width (2.80). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 12. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. chlorolepis* and *S. ontarioensis* (6.919); the smallest separation was between *S. chlorolepis* and *S. randii* (2.278).

Table 12. Between groups F-matrix for the six a priori groups of northeastern taxa (df = 21 68).

Group	*chlorolepis*	*gillmanii*	*glutinosa*	*ontarioensis*	*racemosa*
gillmanii	5.897				
glutinosa	6.343	5.897			
ontarioensis	6.919	4.220	3.989		
racemosa	5.715	3.193	6.043	3.789	
randii	2.278	5.833	4.366	5.982	5.381

Wilks' lambda = 0.0124 df = 21 5 88; Approx. F= 4.6669 df = 105 337 prob = 0.0000

In the Classificatory Discriminant Analysis of 94 specimens of the six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*), percents of correct a posterori assignment to the same a priori group were 75-100%. The Classification matrix and Jackknife classification matrix are presented in Table 13. All 11 specimens of the *S. chlorolepis* a priori group (100%) were assigned a posteriori into the *S. chlorolepis* group; 9 specimens with 97-100% probability and 1 specimen with 78% probability. All 10 of the *S. gillmanii* a priori group were assigned a posteriori to the *S. gillmanii* group: 8 specimens with 93-100% probability, 1 specimen with 89% probability, and 1 specimen with 71% probability. Ten of the 11 specimens of the *S. ontarioensis* a priori group (83%) were assigned a posteriori to *S. ontarioensis* with 91-100% probabilty. One specimen of the *S. ontarioensis* a priori group was assigned a posteriori to *S. glutinosa* with 69% probability (*Morton NA3691* TRT from Tobermory, Ontario; 21 cm tall shoot with small narrow inflorescence). Twenty-eight of the 32 specimens of the *S. glutinosa* a priori group (88%) were assigned a posteriori to *S. glutinosa*; 21 specimens with 90-100% probability, 3 specimens with 88-89% probability, 1 specimen with 77% probability, 1 specimen with 68% probability, 1 specimen with 52% (47% to *S. randii*; *Peirson 647* WAT from Otsego Co., Michigan), and 1 specimen with 40% probability (*Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario). Four specimens of the *S. glutinosa* a priori group were assigned a posteriori to other species:

3 specimens to *S. randii* with 93% probability (*Semple et al. 9368* WAT from McKinley Co., NM), 76% probability (*Peirson 466* WAT from Presque Isle Co., Michigan; 63 cm tall shoot), and 54% probability (40% to *S. chlorolepis*; *Semple & Semple 11239* WAT from Summit Co., Colorado); and 1 specimen to *S. racemosa* with 58% probability (42% to *S. glutinosa*; *Pavlick 80-431* V from 51° 55' N 122° 20' W, British Columbia; Fig. 7; robust plant). Twelve of the 13 specimens of the *S. randii* a priori group were assigned to the *S. randii* group: 9 specimens with 90-100% probability, 1 specimen with 76% probability, 1 specimen with 65% probability, and 1 specimen with 49% probability (49% to *S. chlorolepis*; *Ringius 1760A* WAT from Cadillac Mt., Mt. Desert Is., Maine). One specimen of the *S. randii* a priori group was assigned a posteriori to *S. glutinosa* with 83% probability (*Ringius 1754* WAT from from Cadillac Mt., Mt. Desert Is., Maine). Thirteen of the 16 specimens of the *S. racemosa* a priori group (81%) were assigned a posteriori to *S. racemosa*: 12 specimens with 90-100% probability and 1 specimen with 69% probability. Three specimens of the *S. racemosa* a priori group was assigned a posteriori to other species: 2 specimens to *S. ontarioensis* with 86% probability (*Morton NA4142* TRT from Percé Mt., Gaspésie, Québec) and 50% probability (*Dignard et al. 08-95* QUE from Île-d'Anticosti, Québec; this specimen has the lower stem leaves typical of *S. racemosa*), and 1 specimen to *S. chlorolepsis* with 46% probability (39% to *S. racemosa*; *LaBreque s.n.* MT from Mt. Blanc, Percé, Gaspésie, Québec).

Table 13. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six species level a priori groups using 20 traits; a posteriori placements to groups in rows.

Group	*chlorolepis*	*gillmanii*	*glutinosa*	*ontarioensis*	*racemosa*	*randii*	% correct
chlorolepis	11	0	0	0	0	0	100
gillmanii	0	10	0	0	0	0	100
glutinosa	0	0	28	3	1	3	88
ontarioensis	0	1	1	10	0	0	91
racemosa	1	0	0	2	13	0	81
randii	0	0	3	0	0	12	86
Totals	12	10	31	12	14	15	89

Jackknifed classification matrix

Group	*chlorolepis*	*gillmanii*	*glutinosa*	*ontarioensis*	*racemosa*	*randii*	% correct
chlorolepis	10	0	0	0	0	1	91
gillmanii	1	6	0	0	2	1	60
glutinosa	1	2	19	3	2	5	59
ontarioensis	0	0	3	6	1	1	55
racemosa	1	0	1	2	12	0	75
randii	2	0	3	0	0	9	64
Totals	15	8	26	11	17	17	66

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 94 specimens of *Solidago chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii* are presented in Fig. 31. Eigenvalues on the first three axes were 3.099, 2.200, and 1.040.

Two species level a priori groups analysis: Solidago glutinosa and S. ontarioensis

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits and floral traits. The following traits were included in the analysis: mid stem leaf length, width and number of margin serrations, upper stem leaf number of margin serrations, involucre height, mid series phyllary width, number of ray florets, ray floret lamina width, number of disc florets, disc floret corolla, lobes, ovary/fruit body, and pappus lengths.

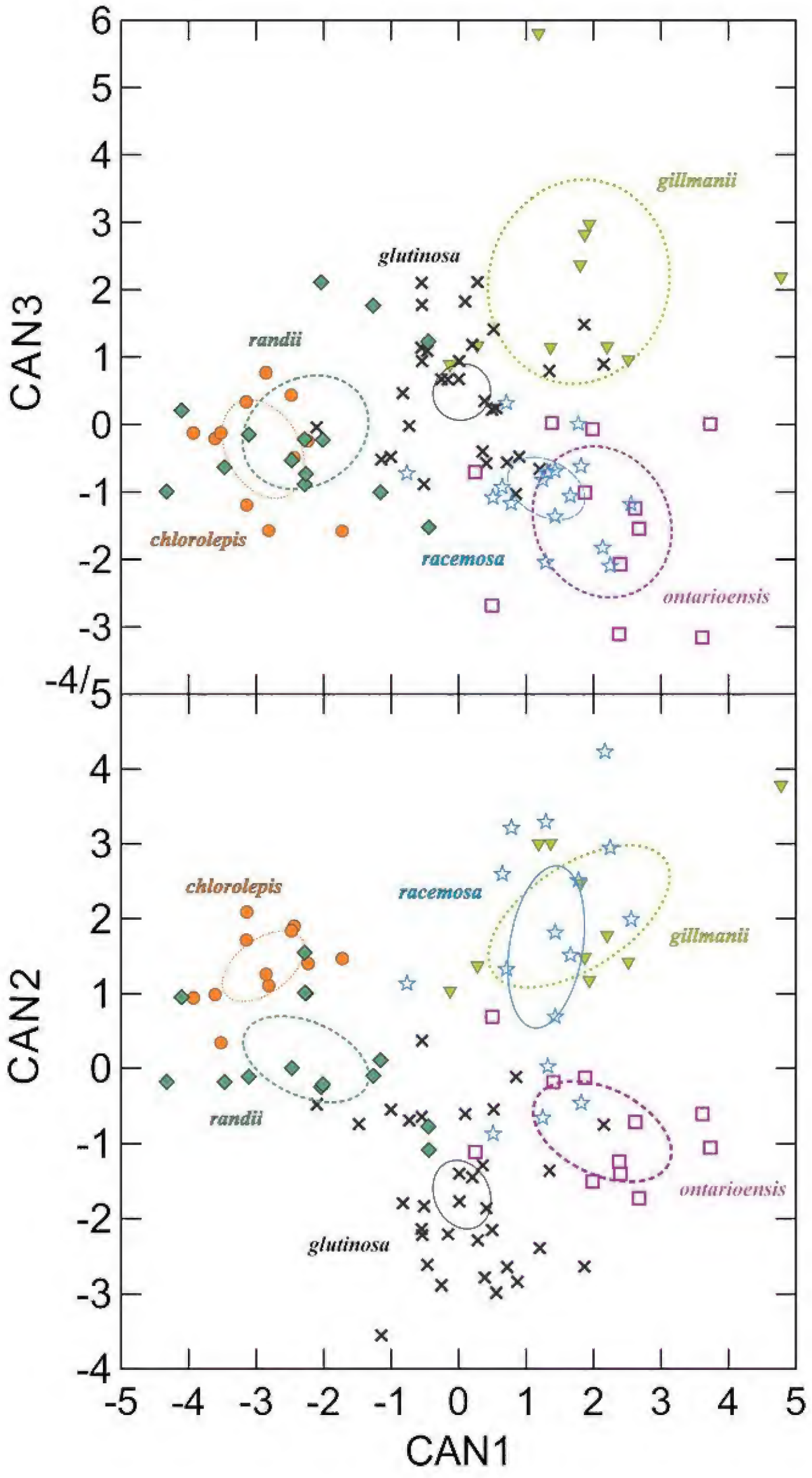

Figure 31. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 94 specimens of northeastern species of *Solidago* subsect. *Humiles* using 21 traits in a COMPLETE analysis: *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black ×s), *S. ontarioensis* (magenta squares), *S. racemosa* (open blue stars), and *S. randii* (green diamonds).

In the STEPWISE discriminant analysis of 47 specimens of two species level a priori groups (*S. glutinosa* and *S. ontarioensis*), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: involucre height (27.53), disc floret ovary/fruit body (23.47), number of disc florets (12.90), and mid stem leaf width (4.11). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago glutinosa* and *S. ontarioensis* had an F-to separate value of 16.419 (Wilks' lambda = 0.3901 df = 1 1 45; Approx. F= 16.4193 df = 4 42 prob = 0.0000).

In the Classificatory Discriminant Analysis of 47 specimens of the two species level a priori groups (*S. glutinosa* and *S. ontarioensis*) plus 1 additional specimen included a posteriori, percents of correct a posterori assignment to the same a priori group were 92% and 91% respectively. The Classification matrix and Jackknife classification matrix are presented in Table 14. Thirty-three of the 36 specimens of the *S. glutinosa* a priori group (92%) were assigned a posteriori into the *S. glutinosa* group; 29 specimens with 91-100% probability, 3 specimens with 83-85% probabily, and 1 specimen with 70% probability. Three specimens of the *S. glutinosa* a priori group were assigned a posteriori to *S. ontarioensis* with 98% probability (*Pavlick 80-431* V from 51° 55' N 122° 20' W, British Columbia; Fig. 7; robust plant), 76% probability (*Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 29 cm tall shoot) and 55% probability (*Morton & Venn NA14175* TRT from Lavoy, Alberta). Ten of 11 specimens of the *S. ontarioensis* a priori group (91%) plus 1 additional specimen were assigned a posteriori into *S. ontarioensis*: 9 specimens with 95-100% probability, 1 specimen with 81% probability, and 1 specimen with 77%. One specimen of the *S. ontarioensis* a priori group was assigned to *S. glutinosa* with 61% probability (*Morton & Venn NA7620* TRT from Flower Pot Is., Bruce Co., Ontario).

Frequencies of CAN1 canonical scores for 48 specimens of *S. glutinosa* and *S. ontarioensis* are presented in histograms in Fig. 32. The Eigenvalue on the first axis was 1.564.

Table 14. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	*glutinosa*	*ontarioensis*	% correct
glutinosa	33	3	92
ontarioensis	1	10	100
Totals	34	12	91

Jackknifed classification matrix

Group	*glutinosa*	*ontarioensis*	% correct
glutinosa	32	4	89
ontarioensis	0	10	91
Totals	33	14	89

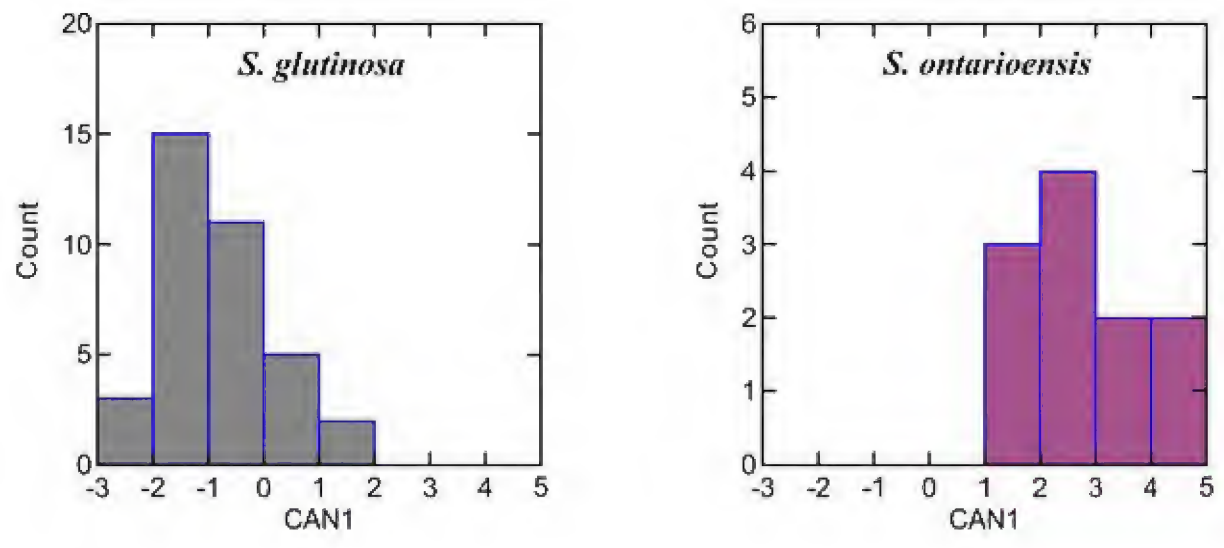

Figure 32. Histograms of CAN1 canonical scores for 48 specimens of *S. glutinosa* (left) and *S. ontarioensis* (right).

Two species level a priori groups analysis: Solidago racemosa and S. randii

The Pearson correlation matrix yielded r > |0.7| for multiple pairs of leaf traits reducing the number to be used to mid stem leaf length and width and upper stem leaf length. Involucre height correlated with mid series phyllary length, ray floret pappus length and disc floret corolla and pappus lengths; involucre height was included in the analysis. Ray floret fruit body and pappus lengths correlated with disc floret fruit body length and disc floret corolla length, respectively; only disc floret ovary/fruit body length was included in the analysis.

In the STEPWISE discriminant analysis of 32 specimens of two species level a priori groups (*S. racemosa* and *S. randii*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc corolla lobe length (26.73), number of peduncle bracts (12.20), and upper stem leaf length (5.64). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago racemosa* and *S. randii* had an F-to separate value of 20.710 (Wilks' lambda = 0.3107 df = 3 1 30; Approx. F= 20.7098 df = 3 28 prob = 0.0000).

In the Classificatory Discriminant Analysis of 32 specimens of the two species level a priori groups (*S. racemosa* and *S. randii*), percents of correct a posterori assignment to the same a priori group were 94% and 87%, respectively. The Classification matrix and Jackknife classification matrix are presented in Table 15. Sixteen of the 17 specimens of the *S. racemosa* a priori group (94%) plus 1 additional specimen included a posteriori were assigned a posteriori into the *S. racemosa* group; 13 specimens with 90-100% probability and 3 specimens with 83-87% probability. One specimen of the *S. racemosa* a priori group plus 1 additional specimen included a posteriori were assigned a posteriori to *S. randii* with 66% probability (*Semple & Ringius 7612*g WAT from York Co., Pennsylvania; a 6.5 cm tall dwarf plant with small leaves; 3 other specimens from the same population was placed into *S. racemosa* with 97-100% probability) and 57% probability (*Peirson 598* WAT from Barbour Co., West Virginia). Thirteen of 15 specimens of the *S. randii* a priori group (87%) were assigned a posteriori into the *S. randii* group; 11 specimens with 96-100% probability and 1 specimen with 74% probability. Two specimens of the *S. randii* a priori group were assigned to *S. racemosa* with 82% probability (*Beaudry 58-2* NY from Smuggler's Notch, Lamoille Co., Vt.; lower stem leaves are broadly lanceolate/winged petiolate and like other specimens of *S. randii*), and 58% probability (*Ringius 1760* WAT from summit of Cadillac Mt., Hancock Co., Maine; a similar shoot of the same collection was placed into *S. randii* with 98% probability).

Frequencies of CAN1 canonical scores for 34 specimens of *S. racemosa* and *S. randii* are presented in histograms in Fig. 33. The Eigenvalue on the first axis was 2.219.

Table 15. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	***racemosa***	***randii***	**% correct**
racemosa	16	1	94
ontarioensis	2	13	87
Totals	18	14	91

Jackknifed classification matrix

Group	***racemosa***	***randii***	**% correct**
racemosa	16	2	94
randii	2	13	87
Totals	18	14	91

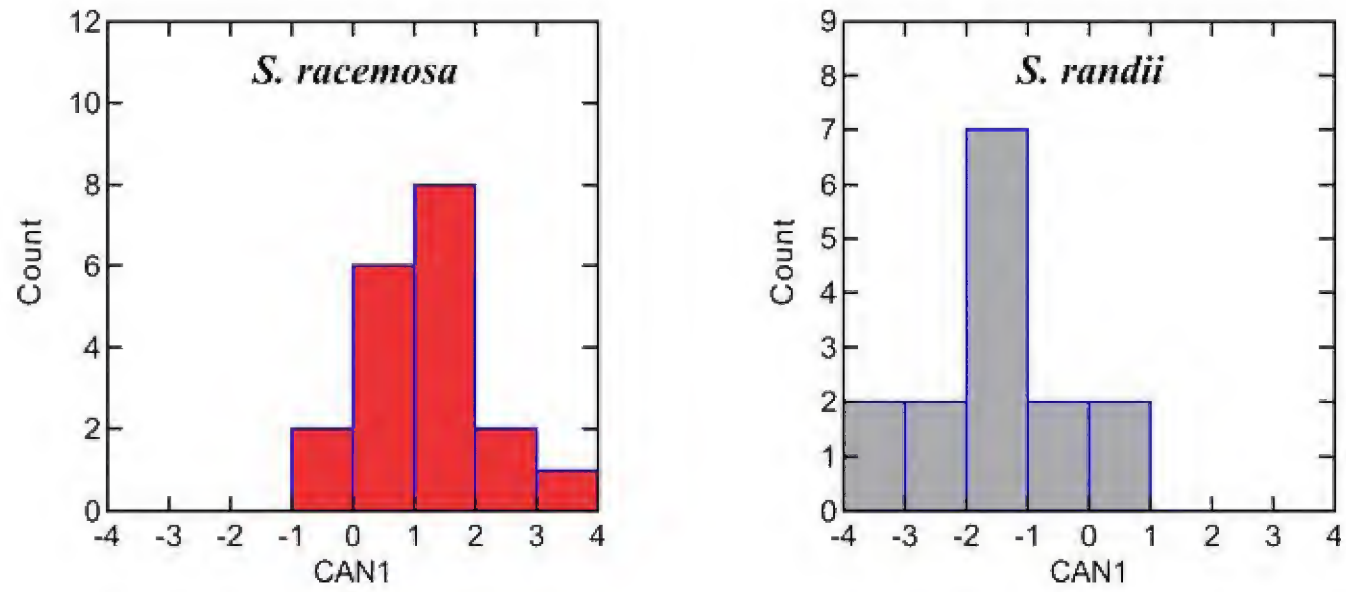

Figure 33. Histograms of CAN1 canonical scores for 34 specimens of *S. racemosa* (left) and *S. randii* (right).

Four southeastern species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for multiple pairs of leaf traits and floral traits reducing the number that could be used. Mid stem leaf length, width, length from widest point to apex, and number of serrations were included in the analysis. Involucre height correlated highly with disc floret pappus length which correlated with mid series phyllary width; involucre height was included in the analysis. Ray floret ovary/fruit body length and ray floret pappus length correlated with disc floret ovary/fruit body length and disc floret pappus length respectively. Ray floret pappus length and disc floret ovary/fruit body length were included in the analysis.

Solidago racemosa was included for comparison because of reports that it is or might be present in Scott Co., Tennessee and northwestern Whitley Co., Kentucky in the range of *S. arenicola*. Specimens from these two counties can have glabrous cypselae like *S. arenicola* in some cases and sparsely strigose cypselae like *S. racemosa* in other cases.

In the STEPWISE discriminant analysis of 49 specimens of four species level a priori groups (*S. arenicola*, *S. kralii*, *S. plumosa*, and *S. racemosa*), the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid series phyllary width (10.57), involucre height (8.25), mid stem leaf width (7.28), number of peduncle bracts (6.00), and ray floret lamina length (5.59). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. F-values based on Mahalanobis distances of the between group centroids are presented in Table 16. The largest separation (F value) was between *S. arenicola* and *S. plumosa* (19.315); the smallest separation was between *S. arenicola* and *S. kralii* (11.215).

Table 16. Between groups F-matrix for the twelve a priori groups in a COMPLETE analysis (df = 5 41).

Group	*arenicola*	*kralii*	*plumosa*
kralii	11.219		
plumosa	19.315	12.639	
racemosa	12.398	10.805	12.500

Wilks' lambda = 0.0616 df = 5 3 45; Approx. F= 13.1384 df = 15 113 prob = 0.0000

In the Classificatory Discriminant Analysis of 51 specimens of the four species level a priori groups (*S. arenicola*, *S. kralii*, *S. plumosa*, and *S. racemosa*) plus 1 additional specimen of *S. austrocaroliniana* and 2 additional specimens of other species included a posteriori, percents of correct a posterori assignment to the same a priori groups were 70-100%. The Classification matrix and Jackknife classification matrix are presented in Table 17. All 17 specimens the *S. racemosa* a priori group (100%) plus 1 specimen included a posteriori were assigned a posteriori to the *S. racemosa* group; 11 specimens with 92-100% probability, 1 specimen with 89% probability, 3 specimens with 71-75% probability, and 2 specimens with 69% probability (18% to *S. kralii* and 8% to *S. arenicola*; *Dignard et al. 08-95* MT from Île-d'Anticosti, Québec) and 63% probability (28% to *S. arenicola*; *Pierson 603* MICH from Nicholas Co., West Virginia). All 10 specimens the *S. plumosa* a priori group (100%) were assigned a posteriori into the *S. plumosa* group; 9 specimens with 98-100% probability and 1 specimen with 69% probability. Eleven of 12 specimens of the *S. arenicola* a priori group (92%) were assigned a posteriori into the *S. arenicola* group; 8 specimens with 95-100% probability (including 1 specimen from Whitley Co., Kentucky and 2 from Scott Co., Tennessee), 2 specimens with 87% and 83% probabilities, and 1 specimen with 72% probability. One specimen of the *S. arenicola* a priori group was assigned a posteriori to *S. kralii* with 46% probability (27% to *S. racemosa* and 20% to *S. arenicola*; *Bailey B150* WAT from Scott Co., Tennessee). Seven of 10 specimens of the *S. kralii* a priori group (70%) plus 1 addition specimen included a posteriori were assigned a posteriori into the *S. kralii* group; 7 specimens with 96-100% probability and 1 specimen with 67% probability. Three specimens of the *S. kralii* a priori group plus 1 additional specimen were assigned a posteriori to other species: 3 specimens to *S. racemosa* with 70% probability (20% to *S. arenicola* and 8% to *S. kralii*; *Semple & B. Semple 11208* WAT from Pulaski Co., Georgia), 69% probability (39 % to *S. kralii*; *Semple & B. Semple 11218* WAT from Aiken Co., South Carolina), and 40% probability (21% to *S. plumosa*, 22% to *S. arenicola*, and 8% to *S. kralii*; *S.B. Jones 15123* USF from Richmond Co., Georgia); 1 specimen was assigned to *S. plumosa* with 64% probability (20% to *S. racemosa* and 15% to *S. kralii*; *Semple & B. Semple 11218* WAT from Aiken Co., South Carolina).

Table 17. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four southern species level a priori groups; a posteriori placements to groups in rows.

Group	*arenicola*	*kralii*	*plumosa*	*racemosa*	% correct
arenicola	11	1	0	0	92
kralii	0	7	1	2	70
plumosa	0	0	10	0	100
racemosa	0	0	0	17	100
Totals	11	8	11	19	92

Jackknifed classification matrix

Group	*arenicola*	*kralii*	*plumosa*	*racemosa*	% correct
arenicola	11	1	0	0	92
kralii	0	5	2	3	50
plumosa	0	0	10	0	100
racemosa	1	0	0	16	94
Totals	12	6	12	19	82

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 52 specimens of *Solidago austrocaroliniana*, *S. arenicola*, *S. kralii, S. plumosa*, and *S. racemosa* are presented in Fig. 34. Eigenvalues on the first three axes were 2.363, 1.312, and 1.087.

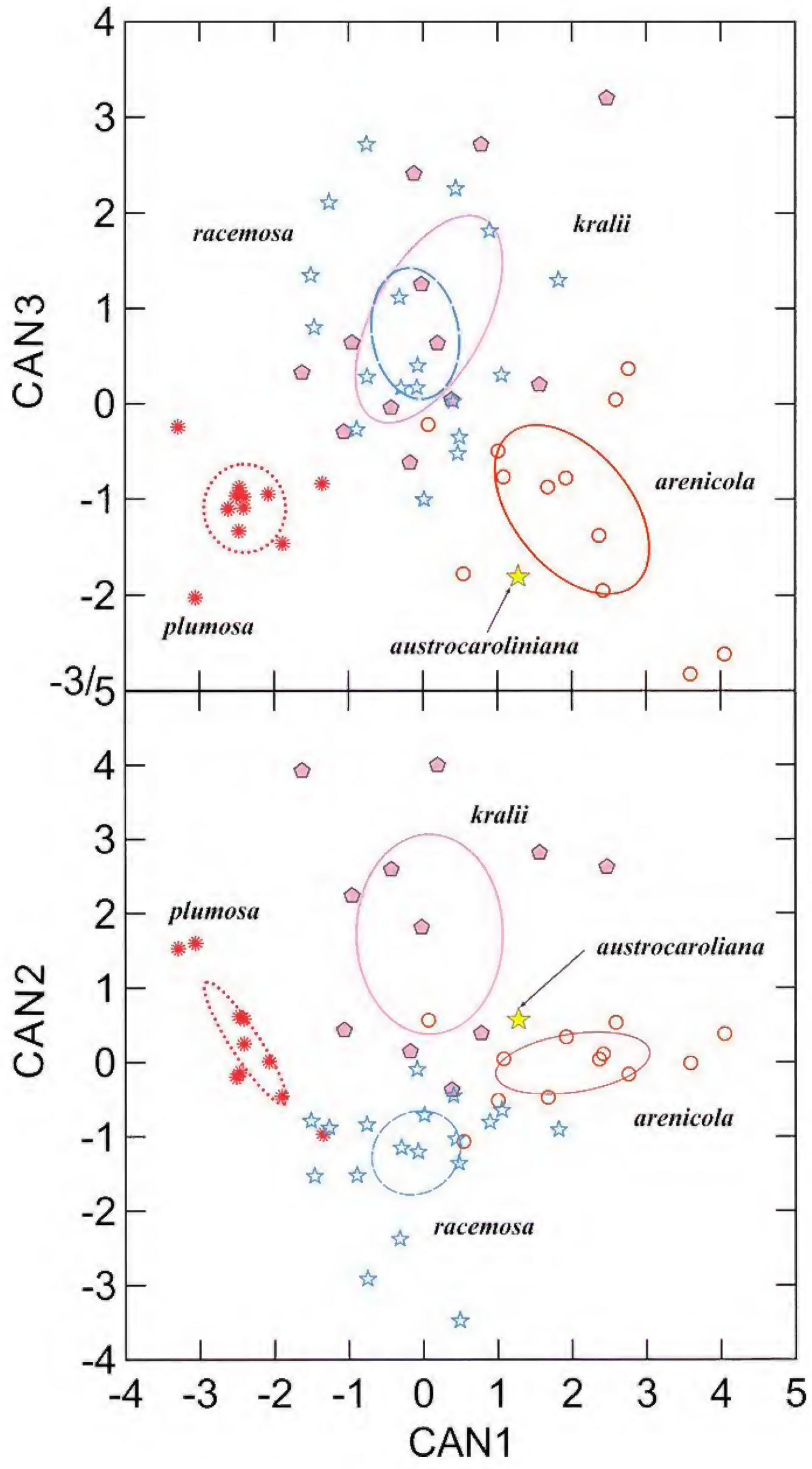

Figure 34. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 52 specimens of *Solidago* subsect. *Humiles*: *S. austrocaroliniana* (yellow stars), *S. arenicola* (red circles), *S. kralii* (pink pentagons), *S. plumosa* (red star-bursts), and *S. racemosa* (open blue stars).

Two species level a priori groups analysis: Solidago arenicola and S. racemosa

The Pearson correlation matrix yielded r > |0.7| for multiple pairs of leaf traits reducing the number to be used to mid stem leaf length, width and serrations. Number of peduncle bracts and the number of nodes in the upper 25% below the inflorescence were included in the analysis. Multiple floral traits were highly correlated and only involucre height, mid series phyllary width, number of ray florets, ray lamina length and width, ray floret pappus length at anthesis, number of disc florets, disc corolla length and lobe length, and disc floret ovary/fruit body length.

In the STEPWISE discriminant analysis of 29 specimens of two species level a priori groups (*S. arenicola* and *S. racemosa*), the following 7 traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: ray floret lamina length (16.35), mid stem leaf width (15.77), upper stem leaf length (10.28), disc corolla length (8.87), lower stem leaf width (7.43), disc floret pappus length (6.51), and involucre height (5.94). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago arenicola* and *S. racemosa* had an F-to separate value of 19.045 (Wilks' lambda = 0.1361 df = 7 1 27; Approx. F= 19.0447 df = 7 21 prob = 0.0000).

In the Classificatory Discriminant Analysis of 29 specimens of the two species level a priori groups (*S. arenicola* and *S. racemosa*), percents of correct a posterori assignment to the same a priori group were 100% and 94%. The Classification matrix and Jackknife classification matrix are presented in Table 18. All 12 specimens of the *S. arenicola* a priori group (100%) were assigned a posteriori into the *S. arenicola* group; 11 specimens with 100% probability (including *Medley 18343-87* KY from Whitley Co., Kentucky) and 1 specimen with 99% probability (*Bailey B150* WAT from Scott Co., Tennessee). Most specimens of *S. arenicola* had glabrous ovaries/disc floret cypselae. Sixteen of 17 specimens of the *S. racemosa* a priori group (94%) plus 1 additional specimen were assigned a posteriori to *S. racemosa*; 16 specimens with 100% probability (including *Peirson 612* MICH from Whitley Co., Kentucky and specimens from several locations in West Virginia) and 1 specimen with 63% probability (*Semple & Ringius 7663c* WAT Montgomery Co., Maryland). One specimen of the *S. racemosa* a priori group was assigned a posteriori to *S. arenicola* with 95% probability (*Gagnon 5059* MT from St-Isadore, Québec; ovaries/disc floret cypselae moderately dense strigose hairs distally and proximally).

Frequencies of CAN1 canonical scores for 29 specimens of *S. arenicola* and *S. racemosa* are presented in histograms in Fig. 35. The Eigenvalue on the first axis was 6.384.

Table 18. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	***arenicola***	***racemosa***	**% correct**
arenicola	12	0	100
racemosa	1	16	94
Totals	13	16	97

Jackknifed classification matrix

Group	***arenicola***	***racemosa***	**% correct**
arenicola	12	0	100
racemosa	1	16	94
Totals	13	16	97

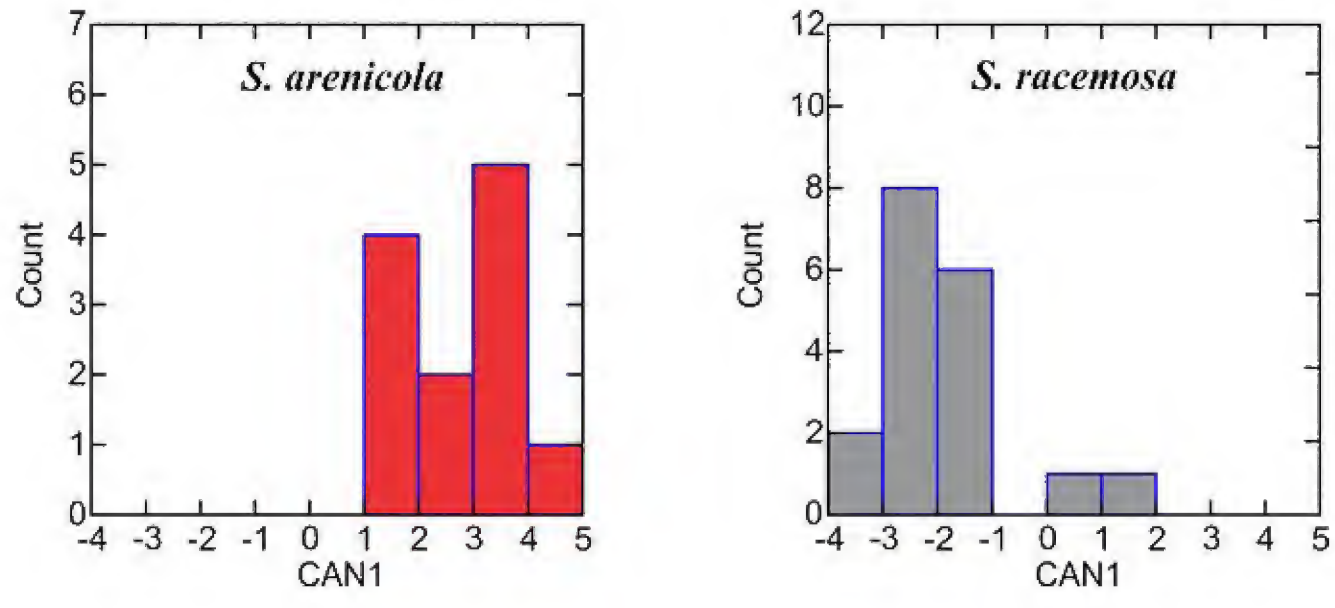

Figure 35. Histograms of CAN1 canonical scores for 29 specimens of *S. arenicola* (left) and *S. racemosa* (right).

DISCUSSION

The results from all the discriminant analyses support the recognition of the following 13 species in *Solidago* subsect. *Humiles*: *Solidago austrocaroliniana*, *S. arenicola*, *S. bellidifolia, S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii, S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*. However, not all *a priori* groups separated strongly in all analyses and the percentages of specimens assigned *a posteriori* to their corresponding *a priori* groups differed considerably and for some specimens the assignment probabilities were low. Overall, the thirteen species are likely closely related and have not diverged greatly in multiple characters in multiple cases. Historically, most of the species have been treated as varieties or subspecies within a single broadly defined transcontinental species, either as *S. spathulata* (Hitchcock and Cronquist 1973), *S. glutinosa* (Cronquist 1947; Ringius 1985), or *S. simplex* (Semple and Cook 2006). Semple and Peirson (2013) concluded that the eastern taxa all deserved species level rank based on the molecular work and species concepts discussions of Peirson et al. (2012) and Peirson et al. (2013). Each species occupies a different ecological niche with some graduation of niches into each other; e.g., lower to mid montane habitats grade into alpine habitats in the Pacific Northwest, and upland and river margin habitats can be very close to each other in the ranges of *S. randii* and *S. racemosa*. *Solidago glutinosa* as delimited here is the only widely distributed species and it shows considerable variation in stem height and leaf size over its range and is the only species that is predominantly diploid but includes some tetraploids in Michigan populations at the eastern limits of its range. While some species are consistently short, e.g., *S. bellidifolia* (4.5-14.5 cm) and *S. chlorolepis* (3.7-19 cm), others range from short to moderately tall, e.g., *S. glutinosa* (7-73 cm), to sometimes very tall for the subsection, e.g., *S. gillmanii* (31-88), *S. plumosa* (20-99 cm), *S. arenicola* (49-103 cm), and *S. kralii* (50-110 cm). Growing conditions greatly influence the final stem height attained in a single season by an individual plant. Even in the same local population stem height has been observed to vary considerable depending upon the amount of soil available in various size rock cracks and crevices, e.g. *S. ontarioensis* along the shore of Lakes Huron and Superior (Fig. 12A) and *S. racemosa* along rivers in Pennsylvania (Fig. 16A) and Maryland. Thus, while stem height was found to be useful in the first two analyses in separating a priori groups, generally stem height can only be used as a secondary character in keys to identification because it can be a misleading trait.

Sets of traits are most useful in distinguishing species in *Solidago* subsect. *Humiles*. However, in the first analysis including all species, the numbers of serrations on upper leaf margins was found to separate *S. spathulata* from other species on the first canonical axis (Fig 24). Multiple species have obvious serrations on basal rosette and lower stem leaves, but only individuals of *S. spathulata* were consistently multi-serrate on the upper stem leaves. *Solidago glutinosa* and *S.*

bellidifolia had lower numbers of upper leaf margin serrations. All three species are western North American taxa. A few collections of eastern *S. gillmanii* and *S. racemosa* also have a few upper leaf serrations. The key to identification of all 13 species presented at the end of this paper uses sets of characters and geography and ecology to separate taxa.

Comments on Basal Rosette and Lowest Stem Leaves

Whether basal rosette and lower stem leaves are the largest or not is often used to split species into groups in the genus overall (e.g., Cronquist 1968; Semple and Cook 2006; Semple 2012). All taxa in *S.* subsect. *Humiles* have basal rosette and lower stem leaves that are the largest on the plant. Characteristics of basal and lower stem leaves have been used in keys to identification of taxa in *S.* subsect. *Humiles* (e.g., Ringius 1985; Semple and Cook 2006). In his doctoral thesis, Ringius (1985) separated the two subspecies of the broadly defined *S. glutinosa* on the basis of whether rosette and lower cauline leaves were spatulate and obtuse to orbicular with rounded apices (diploid subsp. *glutinosa*; here as *S. bellidifolia*, S. *chlorolepis*, *S. glutinosa* and *S. simplex*), or rosette and lower stem leaves were spatulate to obovate and usually sharp tipped (tetraploid subsp. *randii;* here as *S. gillmanii*, *S. ontarioensis*, *S. randii*, and *S. racemosa*). With the development of high resolution digital cameras, a digital library of all collections included in morphological studies such as this one can be created as a quick reference for checking morphological variation on larger structures such as leaves on all specimens included in a taxon. In *S.* subsect. *Humiles*, this became a critical way to compare printed numerical summaries of morphological traits used in the data matrix with the actual specimens even though some were not on hand for direct observation at the time of preparing the key to identification (i.e., some loans had already been returned). The first author's conclusion is that while Ringius (1985) was generally correct about differences between basal rosette and lower stem leaves of different groups of species, the range of variation within some species and even within a single individual was problematic for splitting taxa into groups. All the rosette and lower stem leaves of *S. bellidifolia* and *S. chlorolepis* were generally small for the subsection, narrowly to broadly obovate with more or less rounded apices and with more abruptly to only gradually tapering bases into a petiolate lower portion. This was true for some specimens of *S. glutinosa* although most had more broadly lanceolate leaves with mostly broadly obtuse but pointed apices and tapering leaf bases. Some collections shifted from having the oldest smaller outer leaves in a rosette that matched the first option of the key to having larger inner leaves of the rosette that matched the second option of the key. Even some individuals of *S. gillmanii*, *S. ontarioensis*, *S. randii*, and *S. racemosa* produced a few small outer rosette and lower stem leaves that were apically rounded and not pointed, although most of the larger younger leaves were acute and sharply pointed. Thus, differences in basal rosette and lower stem leaf traits are useful traits to include in keys to *S.* subsect. *Humiles*, but secondary traits, such as cypselae hair characteristics and especially geography and habitat may be critical in moving through the key to the correct identification for a particular specimen. In short, if the collection comes from along a river in the eastern U.S., ignoring those really small spathulate and rounded rosette leaves will get you to *S. racemosa*. If the collection comes from the mountains of northeastern central Mexico, then it is *S. simplex* even if basal leaf traits are confusing. Developing a key to all 13 species was more challenging than expected.

Comments on Western North American Taxa

There are some distinct differences between the four western North American species *S. bellidifolia*, *S. glutinosa*, *S. simplex* and *S. spathulata* and the ranges are fully to mostly allopatric (Fig. 22). *Solidago spathulata*, the California and Oregon coastal dune and headland species is the most distinct of the four western species with its obviously serrate middle (x= 12.7 serrations per side, 6-27 range) and upper stem leaves (x= 7 serrations per side, 2-14 range). *Solidago glutinosa* has few-many to no serrations on its middle (x= 3.6 serrations per side, 0-11 range) and upper stem leaves (x= 0.96 serrations per side, 0-6 range). Vegetative parts and the involucres of *S. spathulata* are usually very obviously resinous compared to the other three western species.

Solidago bellidifolia was treated as *S. glutinosa* var. *nana* by Ringius (1985) and as *S. simplex* var. *nana* in Flora North America (Semple and Cook 2006), but the results from this study indicate that it is both morphologically distinct from *S. glutinosa* and ecologically isolated by occurring at higher elevations in the Pacific Northwest where the ranges of the two species appear to be sympatric (Fig. 22), but are locally allopatric. The basal rosette and lowest stem leaves of *S. bellidifolia* are on average about 3.5 times as long as wide, while those of *S. glutinosa* are on average about 8.2 times as long as wide, although some individuals of *S. glutinosa* can have leaves approach the length to width ratio of those of *S. bellidifolia*. While shoots of *S. bellidifolia* scored for this study were consistently small (x= 9.8 cm, range 4.5-15.5 cm tall), shoots of *S. glutinosa* were generally much taller (x = 35 cm, range 7-63 cm tall). In more stressful habitats, *S. glutinosa* can approach *S. bellidifolia* in stature either at higher elevations in the Rocky Mts. or growing in cracks in rocks along the north shore of Lake Superior in Ontario or near the coast at low elevations on Vancouver Is., British Columbia.

Solidago simplex is treated here as a species limited in distribution to just northeastern central Mexico following Semple, Ma, and Tong (2016) with *S. glutinosa* treated as a separate much more widely distributed species in Canada, the US, and northern Baja California, Mexico (Fig. 22). Earlier, Semple and Cook (2006) had followed Nesom (1989) in treating *S. glutinosa* as a synonym of *S. simplex*. The multivariate analyses of 12 species, the four western species, and just *S. glutinosa* and *S. simplex* presented above provided additional support for treating *S. simplex* and *S. glutinosa* as a species and included more individuals of *S. glutinosa* than had been scored in Semple, Ma, and Tong (2016). Using just three traits (number of disc florets, number of ray florets, and upper stem leaf width), 97% of the 33 *S. glutinosa* specimens included in the two species analysis were assigned a posteriori to *S. glutinosa* and 91% of the 11 *S. simplex* specimens were assigned a posteriori to *S. simplex*. The ranges of the two species are separated by more than 1000 kms. In the first two analyses including 12 and 11 species, a few individuals of other species were assigned a posteriori to *S. simplex* indicating that there are some similarities between *S. simplex* and other species as well as to *S. glutinosa,* at least using the traits selected by the analyses. In reality, it is not likely that there were chance introductions of *S. simplex* individuals into the ranges of *S. ontarioensis* or *S. racemosa*, even if a specimen of each of the latter species happened to have some traits more similar to *S. simplex* than to either eastern species in the first two analyses, in which multiple species were not well differentiated by the traits selected as most suitable to separate the majority of species. In the *S. glutinosa*/*S. simplex* analysis in Semple, Ma, and Tong (2016), number of disc florets, disc floret corolla length, width of the inflorescence, and disc corolla lobe length were selected in a STEPWISE analysis to be useful in separating the two species. While some individuals of *S. simplex* possessed a narrow inflorescence with short peduncles, some had a more open inflorescence with longer inflorescence branches and peduncles (Fig. 20). Only some individuals of *S. ontarioensis* produced more open long-branched inflorescences (Fig. 11), but these were more leafy than those of *S. simplex*.

Comments on northeastern North American Taxa

The collective results of all the multivariate analyses indicate that the six species native to the northeastern US and eastern Canada (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*) are distinct taxa but are more challenging to identify than species from other parts of the range of subsect. *Humiles*. This may be because all five taxa include dwarf individuals and more robust individuals due to differences in growing conditions even within their respective habitats. For example, both plants of *S. glutinosa* from western higher elevation habitats in the Rocky Mts. and from near the shore of Lake Superior in Ontario and plants of *S. ontarioensis* from rocky shores near the eastern Lake Superior and limestone pavements near Lake Huron can be only 10-15 cm tall; small plants have few leaves and very small compact inflorescences. Involucre size is generally smaller in diploid *S. glutinosa* than tetraploid *S. ontarioensis*, but there are rare tetraploids in *S. glutinosa* in Jack Pine barrens of northcentral Michigan where *S. ontarioensis* does not occur.

Ringius (1985) and Semple and Cook (2006) emphasized basal rosette and lower stem leaf traits in their keys to separating the northeastern North American taxa (*S. chlorolepis*, *S. gillmanii*, *S. ontarioensis*, *S. racemosa* and *S. randii*; all treated as varieties within *S. glutinosa* s.l. or *S. simplex* s.l.) from the western North American taxa (*S. bellidifolia*, *S. glutinosa* and *S. simplex*; again all treated as part of *S. glutinosa* s.l. or *S. simplex* s.l.). Rosette and lower stem leaf traits were ultimately retained as useful in the key even though some confusion can arise due to variation in leaf traits even on the same individual. Involucre height differences resulting from being diploid versus tetraploid were not as clear as expected because involucres of tetraploid *S. randii* were smaller than for other tetraploids in some of the plants scored.

The four Gaspésie and Île-d'Anticosti, Québec collections of *S. racemosa* warrant discussion. A collection included in the analyses as a member of *S. racemosa* (*Morton NA4142* TRT from Percé Mt., Gaspésie, Québec) was reported to be diploid (Morton 1981) and was discussed by Ringius (1985) but not assigned to any variety within *S. glutinosa* sensu lato. The specimen was weakly assigned to *S. bellidifolia* (24% probability in the first analysis of 12 species), to *S. ontarioensis* (25% in the second 11 species analysis; 77% probability in the six northeastern species STEPWISE analysis, 48% probability in 21 trait COMPLETE analysis of the northeastern taxa), and to *S. racemosa* (92% probability in the four species southeastern taxa analysis; 77% probability in the *S. racemosa/S. randii* analysis). If the diploid count (Morton 1981) was made from the rootstock of the specimen on the voucher herbarium sheet, then it is the only diploid count for *S. racemosa* and the only diploid count for the *S. gillmanii*, *S. ontarionesis*, *S. racemosa*, *S. randii* group of eastern species. A second collection included in the analyses as a member of *S. racemosa* (*LaBreque s.n.* MT from Mont Ste.-Anne, Gaspésie, Québec) was assigned a posteriori to *S. randii* (53% probability in the first 12 species analysis; 51% probability in the 11 species analysis), to *S. ontarioensis* (86% probability in the six northern species STEPWISE analysis), to *S. chlorolepis* (46% probability in the 21 trait COMPLETE analysis of the northeastern taxa), and to *S. racemosa* (100% in the *S. racemosa/S. randii*) analysis. The ploidy level of *LaBreque s.n.* (MT) is unknown. The two northern most collections of *S. racemosa* were from Île-d'Anticosti, Québec. *Dignard et al 08-95* (QUE) was assigned a posteriori to *S. ontarioensis* (50% probability in the first 12 species analysis; 47% probability in the 11 species analysis; 50% probability in the six northern species 21 trait COMPLETE analysis), to *S. racemosa* (83% in the *S. racemosa/S randii* analysis) and to *S. randii* (31% probability in the six northern species STEPWISE analysis). *Dignard 99-114* (QUE) was assigned a posteriori to *S. racemosa* (36% in the 12 species analysis; 29% probability in the 11 species analysis; 62% probability in the six northern species STEPWISE analysis; 69% in the six northern species 21 trait COMPLETE analysis; and 90% in the *S. racemosa/S randii* analysis). Our conclusion is that all four plants are *S. racemosa* but atypical in some traits for the species, which is not unexpected considering their isolated northern locations. *Solidago chrysolepis* Fern., *S. anticostensis* Fern., *Solidago victorinii* Fern., and *Solidago* × *raymondi* Rousseau (putatively *S. racemosa* × *S. victorinii*) have been proposed for distinctive plants from eastern Québec, but all are treated here as synonyms of *S. racemosa*.

Comments on southeastern North American Taxa

The only species in *S.* subsect. *Humiles* that consistently had more than three peduncle bracts were *S. kralii* and *S. plumosa*. Both species have glabrous ovaries/cypselae bodies. The mid stem leaves of *S. kralii* are 5-7 times as long as wide and those of *S. plumosa* are more linear and 7-21 times as long as wide. Upper stem leaves of *S. kralii* are slight less linear than the mid stem leaves, while those of *S. plumosa* are slightly more linear than the mid stem leaves. Both species usually have very few or no serrations on upper stem leaves. The ranges of the two species are allopatric (Fig. 23) and may be the result of vicariant biogeography of a shared ancestral species.

Solidago racemosa was included in the analysis of the southeastern taxa because Floden (2012) indicated the range of the species (reported as *S. simplex* var. *racemosa*) extends into northern Tennessee and adjacent Kentucky in disjunct populations along separate river systems of the Cumberland Plateau. Floden (2012) cited Peirson et al. (2012) who reported tetraploids of *S. arenicola* in Tennessee. Floden (2012) included comments on *S. erecta* Pursh, which is a member of *S.* subsect. *Squarrosae* A. Gray (Semple et al. 2017) and easily distinguished from members of subsect. *Humiles* by the latter having resinous phyllaries. The resinous quality is produced by minute glands that Floden (2012) noted were not always visible on specimens at 40x. Such glands are often not easily seen even at 70x, but the resin is present and makes the phyllaries shiny at least near the tip. The first author has observed in the process of taking high resolution digital images of all collections included in multivariate analyses of *Solidago* that the light of the camera flash adds white highlights to surfaces that otherwise do not appear to be resinous, but in fact have a thin resinous coating. Adjusting the angle of dissecting scope light can result in the same phenomenon. The phyllaries of *S. arenicola* and *S. racemosa* have a thin resinous coating that reflects light in a few bright spots (Figs. 2F and 16H), while the phyllaries and peduncle surfaces of *S. kralii* are much more obviously resinous (Figs. 10F-G).

Some collections of subsect. *Humiles* from Tennesee and adjacent Kentucky seen during this investigation had glabrous ovaries/fruit bodies and were identified as *S. arenicola*. Some collections had some hairs on the ovary/fruit bodies and were identified as *S. arenicola* on general appearance or as *S. racemosa*. No specimens of *S. arenicola* included in this study were assigned a posteriori to the *S. racemosa* group, and one specimen of *S. racemosa* a priori group was assigned a posteriori to *S. arenicola* with 95% (*Gagnon 5059* QUE from from St-Isadore, Québec; ovaries/disc floret cypselae moderately densely strigose hairs distally and proximally). Both species include tetraploids with larger involucres which may account for the confusion about the identity of the Tennessee/adjacent Kentucky collections. Peirson et al. (2013) included specimens of *S. arenicola* from Kentucky in their cpDNA study including material vouchered as *Peirson 612* (MICH) which was labeled as S104 on their map in their Figure 1. In our multivariate study, *Peirson 612* (MICH) was included as a sample of *S. racemosa* based on the identification on the herbarium sheet label, although the cypselae bodies were completely glabrous. In the two species analysis (*S. arenicola* and *S. racemosa*), *Peirson 612* (MICH) was placed a posteriori into *S. racemosa* with 100% probability and is shown on our map Fig. 23 as being the only Kentucky sample of *S. racemosa*. Four Peirson collections of *S. racemosa* from West Virginia were also included in the our multivariate study and all were assigned a posteriori in the two species analysis to S. *racemosa* with 100% probability. The only collection of *S. arenicola* from Kentucky included in our multivariate study as *S. arenicola* was *Medley 18343-87* (KY; glabrous cypselae bodies) which was placed a posteriori into *S. arenicola* with 100% probability. The three *S. arenicola* collections from Scott Co., Tennessee included in our study all had some short hairs on the distal portion of the ovary/cypselae fruit bodies; these were placed a posteriori into *S. arenicola* with 99-100% probability. Our conclusion is that *S. arenicola* is present in Kentucky and Tennessee and some individuals are either very *S. racemosa*-like in multiple traits (*Peirson 612* MICH) or *S. racemosa* is also present in Kentucky and maybe Tennessee at the same or different locations. These northern populations of *S. arenicola* may just be divergent from the Alabama populations in ovary/cypselae indumenta features and do not include *S. racemosa*. The results of the molecular and morphological studies are contradictory. Further morphological or DNA basal analyses of the populations in Alabama, Tennessee and Kentucky may clarify the matter. If both species are present at the same location then hybridization is possible.

Solidago austrocaroliniana is known only from a single collection. This necessitated that it only be included in the analyses a posteriori and could not be included as a separate a priori group. In the first two analyses, the single specimen of *S. austrocaroliniana* was assigned a posteriori into *S. simplex* (42% and 26% probability respectively; 6% and 0% to *S. arenicola* respectively). In the

analysis of the five southeastern US species, the single specimen of *S. austrocaroliniana* was assigned a posteriori to *S. arenicola* (98% probability); the yellow star symbols for the collection of *S. austrocarolininana* were placed outside the 95% confidence limits ellipses for *S. arenicola*, *S. kralii*, and *S. plumosa*, but closer to *S. arenicola* group centroid. In the protologue of the species Semple (2018) noted that the holotype of *S. austrocaroliniana* looked more like *S. arenicola* than other southeastern species but had smaller involucres. Additional specimens of *S. austrocaroliniana* need to be found in order to resolve questions about its relationships to southeastern taxa of *S.* subsect. *Humiles*.

Key to taxa in *Solidago* subsect. *Humiles*

1 Mid and upper stem leaves with (2-)6-27 serrations; coastal dunes of OR and CA ..... *S. spathulata*
1 Mid and upper stem leaves with very few or no serrations
  2 Peduncles with 4-7 bracts
    3 Mid stem leaves 7-21 times as long as wide; North Carolina ..... *S. plumosa*
    3 Mid stem leaves 5-7 times as long as wide; Georgia, Aiken Co. South Carolina ..... *S. kralii*
  2 Peduncles with 1-3 bracts
    4 Involucres 7–11 mm tall; cypselae glabrous (sometimes sparsely strigose in TN and KY); southeastern KY to northern AL ..... *S. arenicola*
    4 Involucres 3–7(–8) mm; cypselae sparsely to moderately densely strigose
      5 Spring to early summer blooming; upland South Carolina ..... *S. austrocaroliniana*
      5 Summer to fall blooming; western and northeastern North America
        6 Basal rosette and lower stem leaves spathulate to obovate, apices rounded to very obtuse and slightly pointed; stem 2-15(20) cm tall
          7 Basal rosette and lowest stem leaves averaging 3.5-4 times as long as wide; cypselae moderately to moderately densely strigose distally and proximally; high alpine habitats in OR, WA and Vancouver Is., BC ..... *S. bellidifolia*
          7 Basal rosette and lower stem leaves averaging 4-7 times as long as wide; cypselae sparsely to moderate strigose distally and proximally; Mt. Albert region, PQ ..... *S. chlorolepis*
        6 Basal rosette and lower stem leaves spathulate to obovate, apices obtuse with a point to acute and sharply pointed (sometimes rounded in *S. glutinosa*); stem (10-)20-110 cm; high alpine and rock shoreline plants sometimes <20 cm (see *S. glutinosa*, *S. ontarioensis*, *S. racemosa*)
          8 Involuces 4–5.5 mm tall at flowering (larger as fruit develops); western North America, east in Canada to Ontario and Michigan
            9 Basal and lower stem leaves averaging 7-8 times as long as wide; prairie and montane habitats, AK to AZ and NM, east to MI and northern ON ..... *S. glutinosa*
            9 Basal and lower stem leaves averaging 5-6.5 times as long as wide; montane habitats, central Mexico ..... *S. simplex*
          8 Involucres (4.1-)5-8 mm tall; Great Lakes area, uplands, and along rivers from PQ to WV and southeastern KY
            10 Involucres 4.1-5(-5.5) mm tall; cypselae very sparsely to sparsely strigose proximally, more so distally; barren, rocky, non-alpine uplands; se PQ, n. New England, ne. NY ..... *S. randii*
            10 Involucres 5-7 mm tall; cypselae sparsely to moderately strigose or sparsely strigose proximally, to more so distally

11 Cypselae moderately to densely strigose proximally and distally; larger infls open branched; stems 1-4 dm; cauline leaves (2–)4–13(–24); rocky shores, L. Superior, northern L. Huron ..... *S. ontarioensis*

11 Cypselae glabrate to moderately strigose proximally, sparsely to densely so distally; stem to 8 dm tall; cauline leaves often numerous (except for small plants); sand dunes or on rocks near river banks

12 Cypselae glabrate to sparsely strigose proximally, very sparsely to moderately distally; lower cauline leaves usually less than 10 mm wide; calcareous rocky riverbanks, e PQ south to MD and WV and rarely KY ..... *S. racemosa*

12 Cypselae sparsely strigose proximally, sparsely to moderately dense distally; lower cauline leaves usually more than 10 mm wide; sand dunes, L. Michigan, northern L. Huron ..... *S. gillmanii*

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RESUMEN

Se describen e ilustran como especies nuevas **Lithospermum altamiranense** Pat.-Sicil., Cohen, & Pérez-Calix, **sp. nov.**, de la región centro-este del estado de Querétaro y **Lithospermum asteinzae** Pat.-Sicil., Cohen, & Pérez-Calix, **sp. nov.**, del centro de Michoacán. *Lithospermum altamiranense* se diferencia de *L. calcicola* por el menor tamaño de la corola, hasta de 3.5 mm de largo para la primera y hasta de 7 mm para la segunda; y del estilo, de 1.5 mm de largo para *L. altamiranense* y de 2 a 7 mm para *L. calcicola*. En el caso de *Lithospermum asteinzae*, ésta contrasta con *L. oblongifolium* en el menor tamaño de la corola, de 13 mm de largo para la nueva especie y hasta de 30 mm para la ya conocida; en el tamaño de los estambres y su ubicación en el tubo de la corola; además del tamaño del estilo, de 8 mm de largo para *L. asteinzae* y hasta de 28 mm para *L. oblongifolium.* Una vez definidas las especies se les asignó su estado de conservación con base en los criterios de la IUCN.

ABSTRACT

Lithospermum altamiranense Pat.-Sicil., Cohen, & Pérez-Calix, **sp. nov.**, from the central-eastern region of Querétaro, and **Lithospermum asteinzae** Pat.-Sicil., Cohen, & Pérez-Calix, **sp. nov.**, from the center of Michoacan, are described and illustrated as new species. *Lithospermum altamiranense* differs from *L. calcicola* in its smaller corollas and shorter styles. *Lithospermum asteinzae* differs from *L. oblongifolium* in its smaller corollas, shorter styles, and size of the stamens and their location in the corolla tube. Based on IUCN criteria, conservation status for both species is En Peligro (Endangered).

Lithospermum L. (Boraginaceae) está integrado por unas 67 especies y aunque es de distribución cosmopolita, su centro de diversidad se encuentra en el suroeste de los Estados Unidos de América y México, región en la que habitan cerca de 75% de sus especies. En el territorio mexicano se han documentado 48 especies, de las que 36 se catalogan como endémicas. La mayoría se distribuyen en la parte oriental más que en la occidental y tienden a estar restringidas a las regiones montañosas correspondientes a la Sierra Madre Oriental, Sierra Madre Occidental y Eje Neovolcánico, en un intervalo altitudinal de 1300 a 3200 m s.n.m. (Cohen 2018).

Este género, hasta hace poco tiempo, había recibido poca atención de los botánicos. Fue Johnston (1952, 1953, 1954), quien inició el estudio monográfico de *Lithospermum* y sus trabajos son el referente de las floras regionales como las realizadas por Johnston (1962), Nash y Moreno (1981),

Patiño (1985), y Lira-Charco y Ochoterena (2012). En el presente siglo el género fue abordado con un enfoque filogenético y con el uso de marcadores moleculares. Los resultados de Cohen y Davis (2009) recircunscriben al género para incluir en él a distintos taxa americanos de la tribu Lithospermeae (*Lasiarrhenum* I.M. Johnst., *Macromeria* D. Don, *Nomosa* I.M. Johnst. *Onosmodium* Michx., *Perittostema* I.M. Johnst. y *Psilolaemus* I.M. Johnst.), con resultados similares a los obtenidos por Weigend et al. (2009) en su investigación filogenética de *Lithospermum* y afines. Recientemente, Cohen (2018) realizó una detallada monografía del género en México, que es el antecedente directo del presente trabajo, ya que recopila toda la información previa del grupo.

Durante las actividades orientadas a la preparación del fascículo correspondiente a la familia Boraginaceae para la Flora del Bajío y de regiones adyacentes, en el herbario IEB (acrónimo de acuerdo a Thiers continuamente actualizado) del Centro Regional del Bajío, Instituto de Ecología, A.C., se localizaron ejemplares de *Lithospermum* que no se pudieron identificar con el tratamiento taxonómico reciente (Cohen 2108), ni al revisar la literatura especializada ni el material de otras especies depositados en los herbarios que se consultaron.

Debido a que el material botánico depositado en la colección era escaso, se procedió a realizar una búsqueda en los herbarios EBUM, ENCB, MEXU y QMEX, por ser las colecciones donde se sabe que se preservan muestras de la región mencionada. También se efectuaron diversas excursiones, entre junio y septiembre de 2016 y 2017, a las localidades de donde proceden los ejemplares; sin embargo, no fue exitosa la búsqueda en esos lugares, ni en las zonas ecológicamente similares de la región, por lo que se decidió describir las especies con el material disponible. Debe indicarse que en dichas localidades se colectaron otras especies de *Lithospermum* plenamente identificadas, diferentes de las aquí descritas.

Las nuevas especies se compararon con los taxones que presentan mayor similitud morfológica. Finalmente, con los datos del área de distribución, del número sitios de colecta y de la abundancia de las especies objeto de estudio, se procedió a hacer una evaluación de su estado de conservación con base en los criterios de la International Union for Conservation of Nature (IUCN 2012).

LITHOSPERMUM ALTAMIRANENSE Pat.-Sicil., Cohen, & Pérez-Calix, **sp. nov. TIPO: MÉXICO. Querétaro**. Municipio de Cadereyta: 2 km al E de Altamira, Sierra del Doctor, 3000 m, bosque de encino y matorral esclerófilo, 19 Jun 1990, *S. Zamudio y E. Pérez 7939* (holotipo: IEB). Figura 1

Planta herbacea perennis; caules plures ex caudice lignoso oriundi, hispidi ad strigosi; folia sessilia elliptico-lanceolata 1.8–3 cm longa, (0.3)0.4–0.6 cm lata, supra moderate strigosa, subtus pallida et densius strigosa, costa supra submersa, subtus prominenti, venis secundariis non evidentibus; inflorescentiae terminales bracteatae cymosae trichotomae, flores chasmogami, pedicellis 1–1.5 mm longis in fructificatione; calyx segmentis 5 lanceolatis 0.3–0.6 cm longis utrinque strigosis; corolla alba tubulosa extus strigosa sed in dimidio infero glabra, intus glabra, ad faucem glandulis quinis circulatim aggregatis, annulo basali incrassato, lobulis ovatis 0.8 mm longis extus strigosis, intus glabris, tubo 3.5 mm longo, 1.5 mm diametro; stamina 2 mm supra corollae basem inserta, filamentis brevibus minus quam 0.2 mm longis, laminaribus, infra glanduliferis, antheris dorsifixis ellipticis 0.5–0.7 mm longis; stylus cylindricus 1.5 mm longus, stigma terminale; fructus 2 vel 3 clusis 3 mm altis, 2.5 mm diametro, ovoideis albis lucidis dorsaliter verrucosis, superficie ventrali nitida, anguste canaliculata in dimidio superiore, base rotundatis, apice acutis, gynobasis plana ad leviter pyramidalis.

Planta herbácea perenne, hasta 40 cm de altura, tallos varios, que nacen de un caúdice leñoso, verde-amarillentos, ca. 2 mm de diámetro, cilíndricos, algo angulados cuando jóvenes, híspidos a estrigosos, tricomas adpresos, blancos, con la base mineralizada, unos ca. 1 mm de largo y otros ca. 0.3 mm de largo; hojas sésiles, elíptico-lanceoladas, 1.8–3 × (0.3)0.4–0.6 cm, ápice agudo, con un mucrón pequeño, base de ligeramente redondeada a truncada, margen entero, de plano a ligeramente revoluto,

haz moderadamente estrigoso, tricomas rectos, ca. 0.5 mm de largo, envés pálido y muy estrigoso, con la vena media prominente, venas secundarias no evidentes; inflorescencias terminales, bracteadas, cimosas, tricótomas, hasta 7 cm de largo, pedúnculo 1.5–2 cm de largo, raquis hasta 5 cm de largo, con 5 a 8 flores situadas cada 1–1.3 cm, con una bráctea basal, brácteas semejantes a las hojas, 1.3–2 × 0.2–0.4 cm; flores casmógamas, pedicelo 1–1.5 mm de largo en la fructificación, estrigoso, con tricomas cortos y largos; cáliz estrigoso en ambas superficies, acrescente, 0.3–0.4 cm de largo en la floración, 0.4–0.6 cm de largo en la fructificación, dividido en 5 segmentos lanceolados, ápice agudo; corola blanca, tubular, estrigosa externamente de la parte media hacia el ápice, mitad inferior con bandas estrigosas, internamente glabra, con 5 grupos circulares de glándulas en la garganta de la corola, ca. 0.2 mm de diámetro, con un anillo basal engrosado, lóbulos ovados, ca. 0.8 mm de largo, ápice agudo, estrigosos por fuera, con excepción del margen, internamente glabros, tubo ca. 3.5 × ca. 1.5 mm, estambres ubicados ca. 2 mm de la base del tubo de la corola, filamento corto, menos de 0.2 mm de largo, ensanchado o laminar, con glándulas debajo de cada filamento, anteras dorsifijas, elípticas, 0.5–0.7 mm de largo; estilo incluso, cilíndrico, ca.1.5 mm × ca. 0.2 mm, estigma geminado, terminal; fruto esquizocárpico, clusas 2 o 3 por aborción, deprimidas lateralmente, ovoides, ca. 3.0 mm × ca. 2.5 mm, blancas, brillantes, dorsalmente verrucosas, cara ventral lisa, con un canal estrecho de la parte media hasta el ápice en la cara ventral, base redonda, ápice agudo, ginobase de plana a ligeramente piramidal.

Lithospermum altamiranense es semejante en apariencia y en hábito a *L. calcicola*, sin embargo, las diferencias en el tamaño y color de la corola, hasta de 3.5 mm de largo para la primera y hasta de 7 mm para la segunda; el tamaño de los estambres y su inserción en el tubo de la corola; además del tamaño del estilo, de 1.5 mm de largo para *L. altamiranense* y de 2 a 7 mm para *L. calcicola*, entre ambas especies son notables. Estas diferencias se complementan con la mayor longitud de la inflorescencia de *L. altamiranense*, hasta de 7 cm, en contraste con la de *L. calcicola* que mide hasta 15 cm, así como la ornamentación de las clusas, lisas y con pequeñas cavidades en *L. calcicola* y verrucosas en *L. altamiranense* (Cuadro 1).

Distribución y hábitat. *Lithospermum altamiranense* es un elemento endémico del estado de Querétaro, sólo se conoce del Cerro del Espolón, en la cercanía del poblado Altamira, Mpio. Cadereyta, en la región de la Sierra del Doctor. Habita en bosque de encino en transición con matorral esclerófilo, en una ladera rocosa de pendiente pronunciada, a 3000 m s.n.m., con suelo somero y clima templado subhúmedo.

Fenología. Florece y fructifica de junio a julio.

Estado de conservación. *Lithospermum altamiranense* se conoce únicamente del ejemplar tipo; las exploraciones en la zona montañosa del centro y norte de Querétaro, dirigidas a la búsqueda de otras poblaciones, han sido improductivas. Se considera que la especie se puede incluir en la categoría En Peligro (EN), con fundamento en el criterio B, subcriterio 1a y el criterio D (EN, B1a + D) según las categorías y criterios de la Lista Roja de la International Union for Conservation of Nature (IUCN 2012).

Etimología. El epíteto deriva del poblado Altamira, Mpio. Cadereyta, Querétaro, ya que la colecta del espécimen se realizó en sus cercanías.

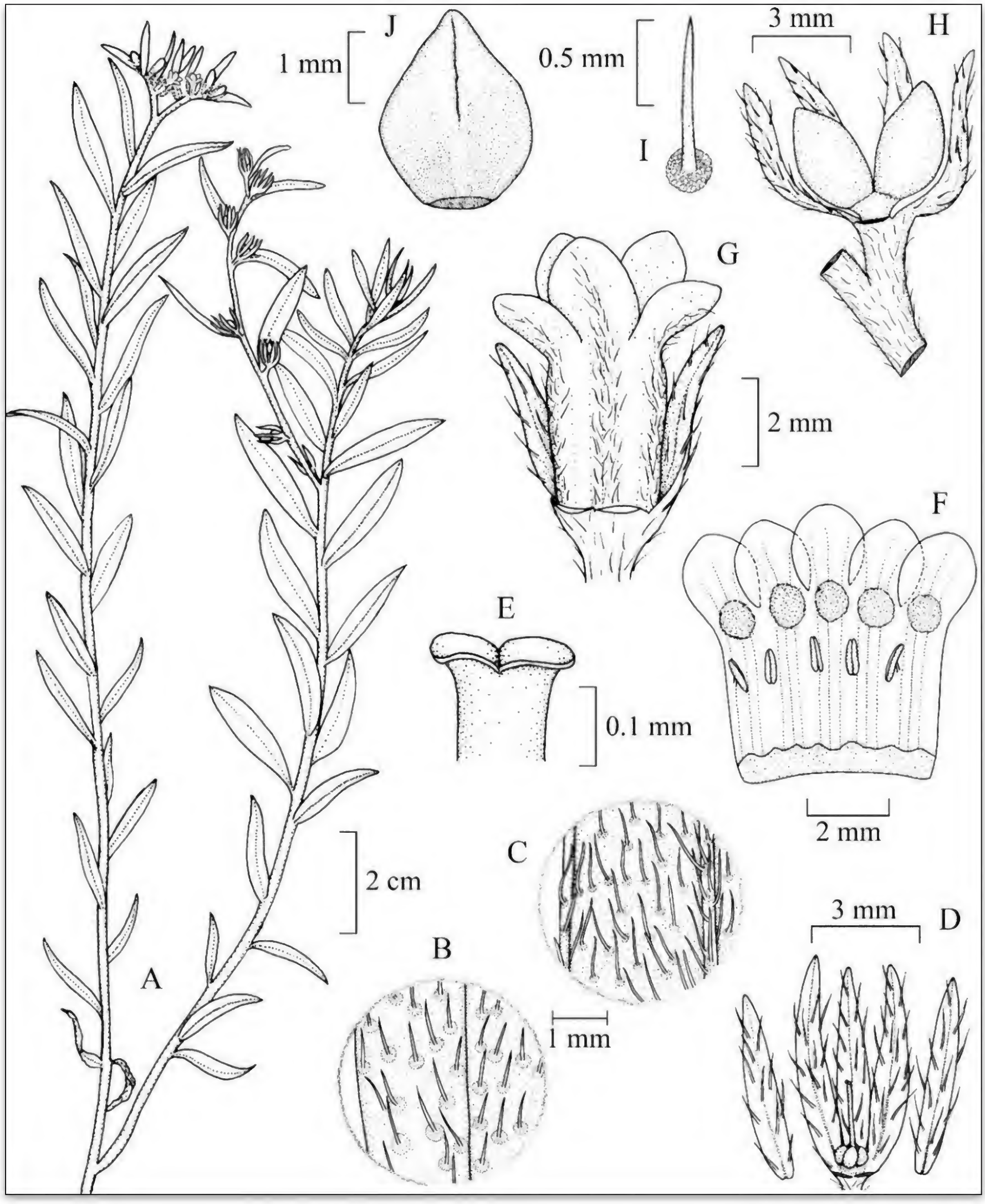

Figura 1. *Lithospermum altamiranense*. A. Aspecto general de la planta. B. Detalle de la superficie estrigosa del haz de la hoja. C. Detalle de la superficie estrigosa del envés de la hoja. D. Sépalos y estilo, con dos sépalos separados. E. Estigma. F. Disposición de los estambres, glándulas y anillo basal en un corte longitudinal de la corola. G. Vista interior de la corola. H. Vista lateral del fruto. I. Tricoma. J. Vista ventral de la clusa. Ilustrado por Manuel Ramírez.

Carácter		*Lithospermum altamiranense*	*Lithospermum calcicola*
Hojas caulinares			
	forma	elíptico-lanceoladas	elípticas a ovadas.
	base	ligeramente redondeada a truncada	redondeada a aguda
	vena media	prominente en el envés	no prominente en el envés
Inflorescencia			
	largo (cm)	hasta 7	hasta 15
	no. de flores por inflorescencia	5-8	6-16
	largo del pedicelo (mm)	1-1.5 mm	0-4(6)
Segmentos del cáliz			
	forma	lanceolados	linear a lanceolados
	largo (mm)	3-4	3-6
Corola			
	forma	tubular	hipocrateriforme
	color	blanca	blanca a amarillenta a blanca con el centro amarillo pálido
	longitud del tubo (mm)	ca. 3.5	3.5-5(7)
	largo lóbulos (mm)	ca. 0.8	1.1-2
	pubescencia	externamente estrigosa, mitad inferior con bandas cortas estrigosas	externamente vilosa, más denso hacia el ápice,
	glándulas	5 grupos circulares en la garganta de la corola	dispersas en la parte superior de la corola
	anillo basal	engrosado	10 cojinetes membranosos
Estambres	inserción	ca. 2 mm de la base del tubo de la corola	3-4 mm de la base del tubo de la corola
	anteras largo (mm)	0.5-0.7	1-1.5
Estilo			
	largo (mm)	ca. 1.5, incluso	2-7.(-8), incluso, algunas veces exserto
Clusas			
	color	blanco	blanco a café oscuro
	ornamentación	dorsalmente verrucosa, con un canal estrecho en la cara ventral	dorsalmente con muchas pequeñas oquedades, con una quilla en la cara ventral

Cuadro 1. Comparación morfológica de *Lithospermum altamiranense* y *L. calcicola*

LITHOSPERMUM ASTEINZAE Pat.-Sicil., Cohen, & Pérez-Calix, **sp. nov. TIPO: MÉXICO. Michoacán**. Municipio de Huiramba: Parte alta del cerro Las Nieves, 3350 m, bosque mixto de *Abies*, *Quercus* y *Pinus*, 17 Jul 1992, *H. Díaz B. y E. García 6991* (holotipo: IEB; isotipo: MEXU). Figura 2.

Planta herbacea perennis erecta; folia sessilia laminis longe lanceolatis (5)6–10(13) cm longis, (0.8)0.9–1.3 cm latis, base decurrentibus vel leviter amplexicaulibus, margine integro interdum revoluto; inflorescentiae terminales, 2 vel 3 per ramum, cymosae breacteatae 4–13 cm longae, pedicellis 1–2.5 mm longis; calyx 5-partitus segmentis lanceolatis 3–4(6) mm longis; corolla pallide lutea, tubulosa-infundibuliformis 10–13 mm longa extus strigulosa sed ad basem glabra, intus glabra, appendicibus faucialibus 1.5 mm longis glandulosis, annulo basali 8–10 pulvinulis, lobis erectis ad leviter reflexis, suborbicularibus ad ellipticis 2.5–3 mm longis; stamina inclusa, filamentis 0.5 mm longis laminaribus, ca. 7 mm supra corollae basem insertis, antheris dorsifixis 1.5–2 mm longis ellipsoideis; stylus 6–8 mm longus, inclusus vel exsertus ad 1 mm supra corollae tubi apicem, stigma terminale; fructus 4 vel minus clusis 2 mm longis luteo-albidis, ovoideis nitidis apice acutis, base rotundatis, interdum ventraliter 1 vel 2 cavas minutas ferentibus.

Planta herbácea perenne, erecta, hasta 50 cm de altura, poco ramificada; tallos café-rojizos, creciendo de un cáudice leñoso, algo lignificados en la base, ca. 3–4 mm de diámetro, estrigosos e hirsutos, con tricomas blanquecinos, ca. 1.2 mm de largo, adpresos, con discos en la base; hojas basales con la base largamente decurrente que aparentan ser pecioladas, hojas caulinas, sésiles, lámina largamente lanceolada, 5–10(13) × 0.8–1.3 cm, ápice agudo, con un mucron endurecido, base decurrente a ligeramente amplexicaule, margen entero, plano o, a veces, revoluto; haz verde, estrigoso, con tricomas blanquecinos, éstos hasta 0.8 mm de largo, adpresos, vena media evidente, venas secundarias no evidentes, envés pálido, estrigoso en la vena media, glabro a esparcidamente estrigoso en el resto de la lámina, vena media y las secundarias evidentes, pero no de manera notable como la central; inflorescencias, terminales, 2–3 por rama, en forma de cimas, bracteadas, 4–13 cm de largo, 6–12 flores por pedúnculo, flores homostilas, pedicelo 1–2.5 mm de largo; cáliz 5-partido, segmentos lanceolados, desiguales entre sí, 3–4(6) mm de largo, exteriormente estrigosos, internamente estrigulosos; corola amarillo-palido, tubular-infundibuliforme, ligeramente ensanchada en el ápice, 10–13 x ca. 3 mm, externamente estrigulosa, con la base glabra, internamente glabra, apéndices fauciales ca. 1.5 mm de largo, con glándulas, opuestas a los lóbulos de la corola, anillo basal presente de 8–10 cojinetes, glabros, tubo 8–9 × ca. 2.5 mm, lóbulos de erectos a ligeramente reflejos, suborbiculares a elípticos, externamente estrigulosos, internamente glabros, 2.5–3 × 2.5 mm; estambres inclusos, alternos a los lóbulos de la corola, filamentos laminares, de 0.5 mm de largo, ubicados ca. de 7 mm de la base de tubo de la corola, con glándulas dispersas en las venas que llegan a los filamentos, anteras dorsifijas, 1.5–2 mm de largo, elipsoides; estilo 6–8 × ca. 0.1 mm, incluso, o si exserto hasta 1 mm por encima del ápice del tubo de la corola; estigma terminal; fruto de 4 o menos clusas, estas ca. 2 mm de largo, de color amarillo-blanquecino, ovoides, lisas, base redonda, ocasionalmente con 1 o 2 pequeños hoyuelos en la parte ventral, ápice agudo

La especie morfológicamente más parecida a *Lithospermum asteinzae* es *L. oblongifolium*; sin embargo, las diferencias entre ellas se observan prácticamente en la mayoría de los caracteres. Las láminas foliares son diferentes en forma, ancho, base margen y en la presencia de las venas secundarias en el haz. Así mismo, se registró mayor longitud en la inflorescencia de *L. asteinzae*, hasta de 13 cm en contraste con la de *L. oblongifolium* que alcanza hasta 23 cm; lo mismo ocurre entre los pedicelos, de 2.5 mm de largo para la primera y hasta de 13 mm para la segunda, y con los segmentos del cáliz de las dos especies, de 4 mm de largo para *L. asteinzae* y de 8 mm para *L. oblongifolium*.

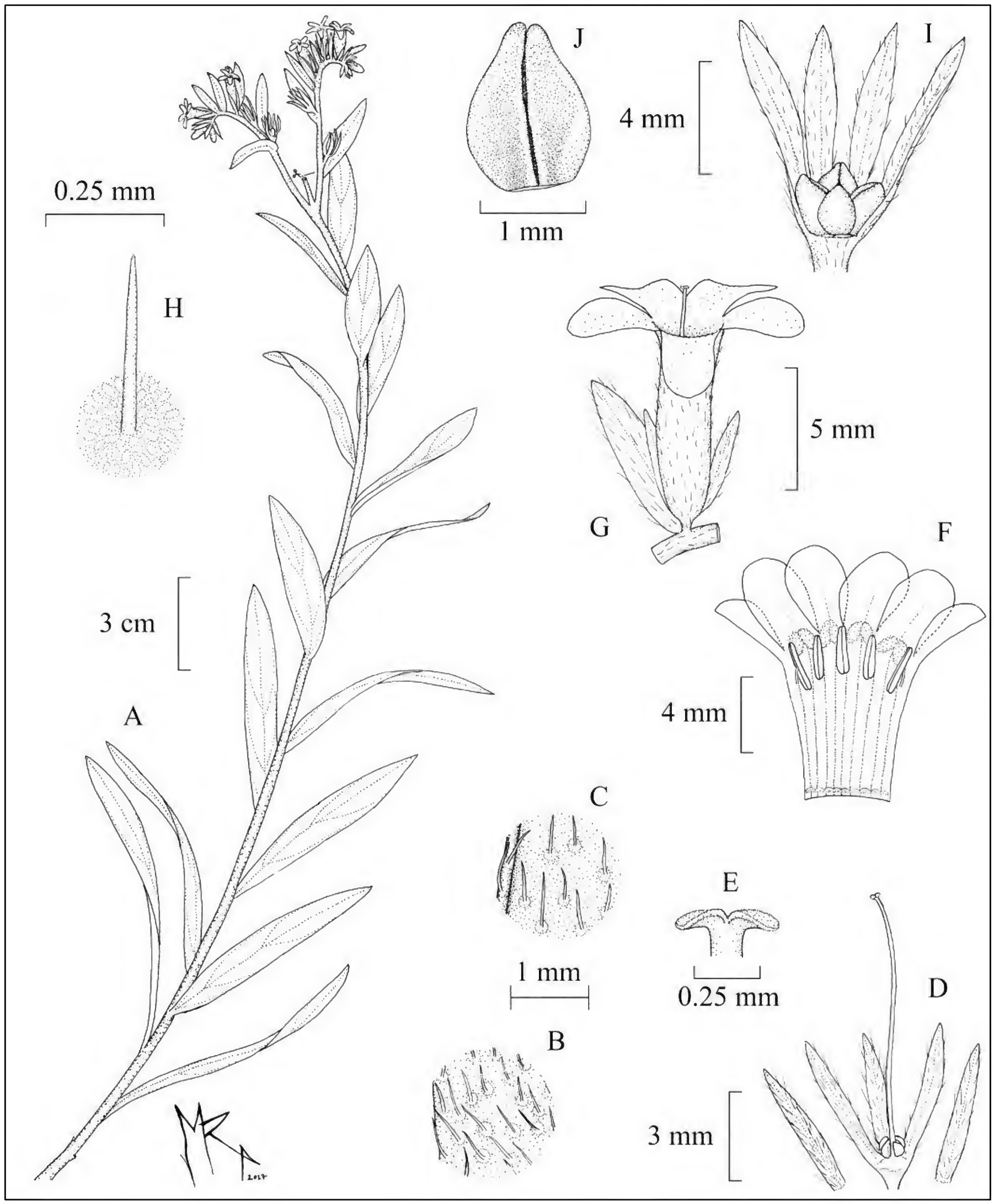

Figura 2. *Lithospermum asteinzae*. A. Aspecto general de un tallo. B. Detalle de la superficie estrigosa del haz de la hoja. C. Detalle de la superficie estrigosa del envés de la hoja. D. Vista interna del cáliz mostrando el estilo y las clusas. E. Vista lateral del estigma. F. Disposición de los estambres y glándulas en un corte longitudinal de la corola. G. Vista exterior de la corola, con dos sépalos retirados. H. Tricoma. I. Vista lateral del fruto tetralobado. J. Vista ventral de la clusa. Ilustrado por Manuel Ramírez.

Otras diferencias notables entre ambos taxa se presentan en el tamaño de la corola, de 13 mm de largo para la nueva especie y hasta de 30 mm para la ya conocida; en el tamaño de los estambres y su ubicación en el tubo de la corola; además del tamaño del estilo, de 8 mm de largo para *Lithospermum asteinzae* y hasta de 28 mm para *L. oblongifolium*; las disimilitudes se complementan con la ausencia de anillo basal en *L. oblongifolium* en contraste con el anillo de 8 a 10 cojinetes o rebordes que se observa en *L. asteinzii* (Cuadro 2).

Carácter		*Lithospermum asteinzae*	*Lithospermum oblongifolium*
Láminas foliares caulinares	forma	largamente lanceoladas	elípticas a ovadas
	largo (cm)	(5)6-10(13)	2–12(–14)
	base	decurrente a ligeramente amplexicaule	redonda a aguda
	margen	plano a revoluto	plano
Inflorescencia	posición	solo terminal	terminal, raramente axilar
	largo (cm)	4-13	hasta 15 (28)
	pedicelo largo (mm)	1-2.5	4 a 13 (19)
Cáliz	Segmentos forma	lanceolados	linear-lanceolados
	largo (mm)	3-4(6)	5 a 8(-20)
	color	amarillo-pálido	amarilla o verde-amarillenta.
Corola	largo (mm)	11-13	20 a 45.
	largo del tubo(mm)	8-9	(16)20 a 37
	anillo basal	8-10, glabro	ausente

Cuadro 2. Características diferenciales entre *Lithospermum asteinzae* y *L. oblongifolium*

Distribución y hábitat. *Lithospermum asteinzae* es una especie endémica de la zona templada de Michoacán, donde se ha colectado en los municipios Huiramba y Tingambato, en la provincia fisiográfica Faja Volcánica Transmexicana. El tipo de vegetación corresponde al bosque mixto de oyamel, encino y pino ubicado en una ladera rocosa con pendiente pronunciada, en altitudes entre 3200 y 3350 m, con suelos profundos y clima templado.

Fenología. Florece y fructifica de julio a septiembre

Material adicional examinado. MÉXICO. Michoacán. Municipio de Tingambato: Parte alta del Cerro el Chivo, bosque de *Pinus* y *Alnus* con abundantes gramíneas amacolladas, 3200 m, 7 Sep 1989, *Díaz y Pérez 5978* (IEB, MEXU).

Estado de conservación. *Lithospermum asteinzae* se conoce de dos ejemplares; la búsqueda de otras poblaciones en el Cerro las Nieves, en el Cerro el Chivo y en otras cimas de la región ecológicamente similares resultó infructuosa. Se propone ubicar a *L. asteinzae* en la categoría de En

Peligro (EN), con base en el criterio B, subcriterio 1a y criterio D (EN, B1a + D) según las categorías y criterios de la Lista Roja de la International Union for Conservation of Nature (IUCN, 2012)

Etimología. El epíteto está dedicado a Gaiska Asteinza Bilbao, maestro sustancial y duradero, pero sobre todo formador de individuos críticos.

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DOS ESPECIES NUEVAS DE *LONCHOCARPUS* (LEGUMINOSAE) DE LA SIERRA MADRE ORIENTAL, MÉXICO

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RESUMEN

Se describen e ilustran **Lonchocarpus scorpioides** M. Sousa ex Cruz Durán & Andrade, **sp. nov.**, y **L. necaxensis** Miranda & Sousa ex Cruz Durán & Andrade, **sp. nov**., endémicas de la Sierra Madre Oriental, México, y son asignadas a la sect. *Densiflori*. *Lonchocarpus scorpioides* es similar a *L. santarosanus* Donn. Sm., sin embargo, difiere de este último por presentar hojas con menor número de folíolos, inflorescencias con braquiblastos más cortos, pero con mayor número de flores, bractéolas más cortas y lineares y flores más pequeñas. Se discute además su posible relación con el género *Derris* Lour. *Lonchocarpus necaxensis* se distingue por sus folíolos con ápice largamente caudado, dientes del cáliz triangular-agudos a lineares, (2–)3–4 mm de largo, androceo pseudomonadelfo, frutos globosos y semillas globosas o subesféricas a reniformes.

ABSTRACT

Lonchocarpus scorpioides M. Sousa ex Cruz Durán & Andrade, **sp. nov.**, and **L. necaxensis** Miranda & Sousa ex Cruz Durán & Andrade, **sp. nov.**, endemic to the Sierra Madre Oriental, Mexico, are described and illustrated. Both species are asigned to sect. *Densiflori*. *Lonchocarpus scorpioides* is similar to *L. santarosanus* Donn. Sm. but differs from it in its leaves with fewer leaflets, inflorescences with shorter brachyblasts but with a greater number of flowers, shorter and linear bracteoles, and smaller flowers. A possible relationship with the genus *Derris* Lour. is discussed. *Lonchocarpus necaxensis* is distinguished by its leaflets with long caudate apex, calyx teeth triangular-acute to linear, (2–)3–4 mm long, pseudomonadelphous androecium, globose fruits, and globose or subspherical to reniform seeds.

El género *Lonchocarpus* Kunth (Leguminosae, Papilionoideae), miembro de la tribu Millettieae, incluye alrededor de 180 especies neotropicales y una más en la costa occidental de África ecuatorial (Sousa 2009a, 2009b, 2010; Sousa et al. 2014). En el proceso de revisión de material botánico en el Herbario Nacional de México (MEXU), perteneciente al género *Lonchocarpus*, para su tratamiento en la Flora del Bajío y de regiones adyacentes, se detectaron ejemplares de la región conocida como Huasteca Mexicana, y pertenecientes a la sect. *Densiflori* Benth. Se distinguen dos entidades, que no corresponden a alguno de los taxa hasta ahora conocidos del género *Lonchocarpus*. Estos ejemplares ya habían sido revisados y analizados por Mario Sousa Sánchez† [1940–2017] (Grether 2017), quien inició el estudio taxonómico de *Lonchocarpus* para la Flora del Bajío y determinó estos ejemplares botánicos como pertenecientes a dos especies nuevas. Se ha corroborado la determinación de Mario Sousa y se describen aquí como especies nuevas para la ciencia.

LONCHOCARPUS NECAXENSIS Miranda & Sousa ex Cruz Durán & Andrade, **sp. nov**. **TIPO**: **MÉXICO**. **Puebla**. Mpio. Juan Galindo: Orillas del río Necaxa, al N de Huauchinango, 27 marzo 1945 (flor), *A.J. Sharp* y *F. Miranda 3442* (holotipo: MEXU!; isotipo: MEXU!). Figura 1.

Foliolorum apice longe caudato, calycis dentibus triangulari-acutis vel linearibus (2–)3–4 mm longis, androceo pseudomonadelpho, fructibus globosis, et seminibus globosis vel subsphaericis ad reniformibus distinguit.

Árboles (1.5–)2–8(–10) m de alto o arbustos semirastreros (0.7–)1–5 (–6) m de alto; corteza interna sin fluido en el corte; ramillas densamente tomentosas, indumento pardo a canescente, con lenticelas circulares a elípticas, de color crema. **Hojas** (11–)13–26.5(–29) cm de largo, con filotaxia dística en brotes nuevos y posteriormente con arreglo helicoidal por torsión de tallos en las ramas con hojas maduras; estípulas 1.5–2 × 0.7–1 mm, deciduas, triangulares; pecíolos 2.5–6.8(–8) cm de largo, teretes, ligeramente estrigosos; raquis 2.5–5 cm de largo, terete, tomentoso; peciólulos 3–5 mm de largo, pulvinulados, glabros, pilosos cuando jóvenes; folíolos (3–)5(–7), (5.2–)6.8–12.6(–13.2) × (2.4–)3–5.6 (–6.3) cm, elípticos a brevemente ovados, membranáceos, epunteados, el haz seríceo a glabro, el indumento canescente, con venación reticulada evidente, el envés densamente estrigoso, canescente, la base cuneada, el margen plano, el ápice largamente caudado hasta 2 cm de largo; venas secundarias principales 6–7(–8) por lado, venación camptódroma. **Inflorescencias** en pseudoracimos axilares, (3–)4–8(–9.5) cm de largo; floración coetánea; pedúnculos (0.5–)1–3.6(–4.6) cm de largo, ferrugíneos a amarillentos; raquis ferrugíneo a amarillento; pedúnculos florales 3–7 mm de largo, ferugíneos a amarillentos; pedicelos (4–)5–6(–7.5) mm de largo, ferrugíneos a amarillentos; brácteas pedunculares 0.8–1 mm de largo, lineares, brácteas pedicelares deciduas; bractéolas (1–)2–2.5 mm de largo, lineares, opuestas, adpresas al cáliz en botón, posteriormente distantes del cáliz, en el 1/4 a 1/3 superior del pedicelo, pubescentes. **Flores** 1.3–1.4 cm de largo, azules, lila claro, lila, guinda, morado con blanco, moradas, violeta o rosadas; cáliz con tubo 3–3.5 × 5 mm, ferrugíneo a amarillento y la parte superior interna serícea, 5–dentado, dientes triangular-agudos a lineares, el carinal (2–)3–4 mm de largo, en botón evidentemente curvados; estandarte con lámina 1.1–1.2 × 1–1.1 cm, suborbicular, ápice brevemente emarginado, sin aurículas basales, el lado externo seríceo, canescente, la base callosa, las callosidades decurrentes en la uña, ésta 1.7–3 mm de largo; ala con lámina 9–10 × 3–4 mm, pubescente hacia el ápice, oblonga a falcada, aurícula reducida, uña 4–4.5(–5) mm de largo; pétalos de la quilla con lámina 8.5–10 × 3.5–4.5 mm, subfalcada, pubescente en el ápice hacia la parte carinal, uña 4–4.5 mm de largo; androceo 13–14 mm de largo, pseudomonadelfo; pistilo 12 mm de largo, ovario 7.5 mm de largo, densamente seríceo, canescente, con 2–3 óvulos, estilo ca. 4.5 mm de largo, incurvado, glabro, estigma capitado. **Fruto** (2.8–)3.2–5.5(–7) × 1.8–2.8(–3) cm, globoso, elíptico a ovado, lateralmente comprimido, café a amarillo, velutino, generalmente con 1(–2) semillas, el borde vexilar más pronunciado, sutura vexilar 2 mm de grosor, trinervada, sutura carinal 1.5 mm de grosor, tardíamente dehiscente solo por el margen vexilar, ápice redondeado y rostrado. **Semillas** 1.4–2 × 1–1.2 × 1–1.3 cm, globosas o subesféricas a reniformes, negras a castaño oscuro o rojo cereza. **Plántulas** con cotiledones hipogeos y eofilos 1-foliolados, opuestos.

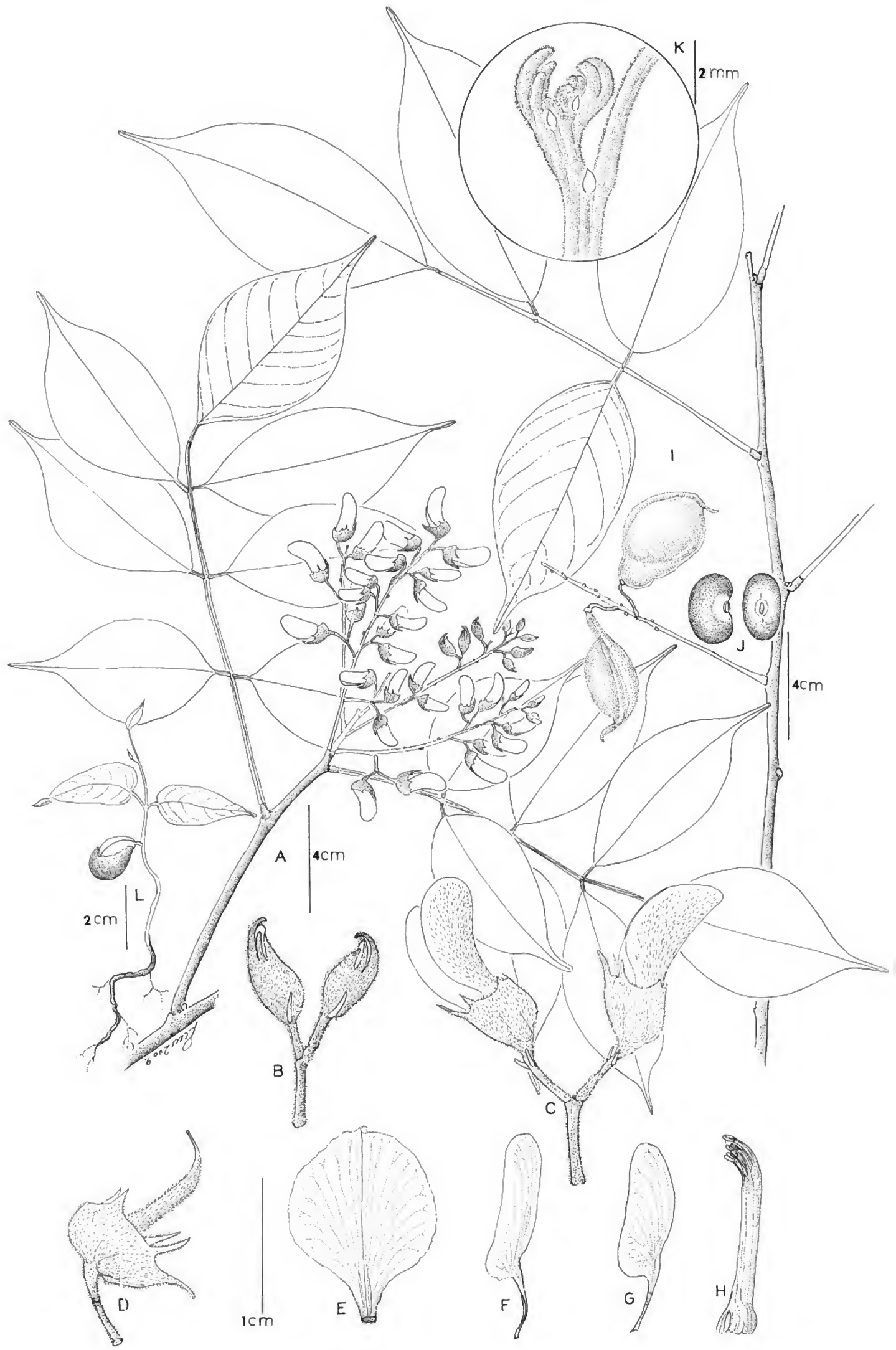

Figura 1. *Lonchocarpus necaxensis*. A. Rama con pseudoracimos. B. Botones florales. C. flores y bractéolas. D. Cáliz y pistilo. E. Estandarte. F. Ala. G. Pétalo de la quilla. H. Androceo. I. Rama con frutos. J. Semilla, vista lateral y ventral. K. Estípulas. L. Plántula. (A, D–H, *Sousa* y *Tenorio 13372*, MEXU; B, *Luna* et al. *1903*, MEXU; C. *Sharp* y *Miranda 3442*, MEXU; I–J. *Rubio 191*, MEXU; K. *Rzedowski 48414*, MEXU; L. *Hernández* y *Tenorio 7112*, MEXU). Ilustración por Ramiro Cruz Durán.

Ejemplares adicionales examinados. MÉXICO. San Luis Potosí. Mpio. Xilitla: 2 km NE Ejido Xilitlilla, *Rzedowski 10519* (ENCB). **Querétaro.** Mpio. Landa: 1.5 km al SE de La Yesca, *Rubio 1581* (IEB), *2512* (MEXU, MO); Puerto de Los Cajones, ± 4 km al NO de La Yesca, *González 318* (MEXU); Puerto de Los Cajones, ± 3 km al O de La Yesca, *González 581* (MEXU); El Banco, 1.5 km al poniente de El Puerto Hondo, *Rubio 539* (MEXU), *Tenorio* y *Rubio 19200* (FCME, IEB, MEXU); 1.5 km al SE de La Yesca, *Rubio 2317* MEXU); 1 km al O de El Puerto del Sabino, *Rubio 191* (MEXU); 1 km al SE de El Pemoche, *Rubio 2300* (MEXU); 2 km al poniente de El Humo, *Rubio 101* (MEXU); cañada al E de Puerto Hondo, camino a la Yesca, *Tenorio* y *Rubio 19194* (FCME, IEB, MEXU). Mpio. Pinal de Amoles: 1 km de San Pedro El Viejo, rumbo a La Colgada, *Cervantes 84* (FCME, IEB; MEXU); cerca de Huazmazantla, 13 km al NE de Pinal de Amoles, sobre carretera a Jalpan, *Rzedowski 48414* (MEXU); 4 km al NE de San Pedro El Viejo, sobre el Camino a La Yerbabuena, *Rzedowski 43004* (MEXU); 12 km al NO de Pinal de Amoles, *Tenorio* y *Hernández 345* (FCME, MEXU). Mpio. Arroyo Seco: Aproximadamente 1 km de El Jardín, camino a La Florida, *Carranza 1647* (MEXU); 1 km de El Jardín, camino a La Florida, *Tenorio 19183a* (MEXU). **Hidalgo**. Mpio. Tlanchinol: 9 km al N de Quetzalcingo, *Ochoa 974* (ENCB, MEXU); 7.2 km al SO de Tlanchinol, carretera 105, *Bartholomew* et al. *3436* (ASU, MEXU). Mpio. Xochicoatlán: Malila, *Puig 4598* (ENCB, MEXU). Mpio. Eloxochitlán: 9 km al O de Ixmolintla, camino a Almoloya, *Martínez* y *Samain 42518, 42519* (IEB, MEXU), *42520* (MEXU), *42521* (FCME, IEB, MEXU); 3 km al S de Eloxochitlán, *Trejo 201* (MEXU); Eloxochitlán, 4.5 km al E, *Alcántara* y *Mayorga 2953* (MEXU); Ototlán, km 9.5 del camino de terracería a Eloxochitlán, *Alcántara* y *Ortíz 1990* (MEXU), *Luna* et al. *2561* (FCME, IEB, MEXU); Eloxochitlán, km 9.5 de camino de terracería, *Alcántara 2244* (FCME, MEXU); Eloxochitlán, km 5 del camino de terracería, *Luna* et al. *1903* (FCME, MEXU); 5 km al S de Eloxochitlán, *Hernández* y *Tenorio 7112* (FCME, IEB, MEXU); desviación a Eloxochitlán, P02, *Alcántara* y *Mayorga 2741* (FCME, IEB, MEXU); camino a Eloxochitlán, km 9, *Alcántara 2940* (FCME, MEXU); Eloxochitlán, km 9 del camino de terracería, *Alcántara* y *Ortíz 2139* (FCME, IEB, MEXU). Mpio. Juárez-Hidalgo: Iztacoyotla. 15 m al N de Juárez-Hidalgo, *Hernández* et al. *6106* (MO). Mpio. Molango: 3 km al SO de Molango, *Pérez 582* (MEXU); 1.7 km el E del km 123, Pachuca-Tampico, al E de Molocotlán, *Mayorga* y *Alcántara 175* (FCME, IEB, MEXU), Lago Atexca, debajo de Molango, *Moore 3477* (GH). Mpio. Mezquititlán: Los Venados, *Puig 4558* (MEXU). **Puebla**. Mpio. Pahuatlán: Xopanapa, 8 km al SO de Pahuatlán y 11 km al NE de Honey, *Tenorio* y *Romero de T. 11376* (FCME, IEB, MEXU), *Tenorio 19193, 19434* (MEXU), *Campos* et al. *242* (MEXU); 0.53 km al OSO de Xopanapa, camino a Acahuatlán, *Martínez* y *Ramos 41588* (FCME, IEB, MEXU); Xopanapa, 10 km al E de Honey, *Sousa* y *Tenorio 13372* (FCME, IEB, MEXU); Acahuales, *Tenorio* y *Ramos de T. 11385* (MEXU). Mpio. Juan Galindo: Along Rio Necaxa, near Huauchinango, *Sharp* y *Miranda 45365* (MICH). **Veracruz.** Mpio. Huayacocotla: El Salto en Helechos, *Ballesteros* y *Morales 194* (ENCB, MEXU, XAL). Mpio. Xilotepec: Cerro Cuajitole, *Castillo* et al. *17543* (XAL). Mpio. Naolinco: La Cascada, *Ventura 12839* (ASU, ENCB, MEXU, XAL).

Distribución. Se distribuye en los estados de San Luis Potosí, Querétaro, Hidalgo, Puebla, y Veracruz; también se espera encontrarla en el sur de Tamaulipas, pues esa región forma parte de la Huasteca Mexicana.

Hábitat. Es un componente importante del bosque mesófilo de montaña primario y secundario, bosque caducifolio-*Pinus*, bosque de *Quercus*-*Pinus*, bosque de *Liquidambar*-*Quercus*, bosque de *Quercus*, bosque de *Quercus*-cedro, bosque de *Pinus*-*Quercus* y *Cupressus*, bosque de *Pinus*-cedro blanco y *Quercus*, selva baja caducifolia y selva mediana perennifolia. Se presenta en suelos pardos, amarillos, rojizos, negros, arcillosos, profundos y pedregosos con hojarasca, en laderas calizas y sitios rocosos, en altitudes de (1040–)1240–2000 m. Su asociación más frecuente es con Verbenaceae, *Senecio* sp., y *Pinus* spp.

Fenología. Florece de marzo a mayo y fructifica de mayo a octubre, escasamente en noviembre.

Nombre común. En el estado de Querétaro se le conoce como frijolillo.

Afinidades. *Lonchocarpus necaxensis* se ubica en la sect. *Densiflori* Benth. de acuerdo con Sousa (2005) y se distingue por presentar folíolos con ápice largamente caudado, dientes del cáliz triangular-agudos a lineares, (2–)3–4 mm de largo, androceo pseudomonadelfo, frutos globosos y semillas globosas o subesféricas a reniformes.

Etimología. El epíteto específico hace referencia al río Necaxa en el estado de Puebla, uno de los sitios donde se colectaron por primera vez ejemplares de esta especie por Faustino Miranda y A. J. Sharp. Este nombre específico aparentemente fue sugerido por Faustino Miranda † [1905–1964], botánico español, exiliado en México y estudioso de la flora mexicana (Dosil et al. 2001), y probablemente, Mario Sousa Sánchez quiso conservar el nombre, dando crédito al destacado investigador.

LONCHOCARPUS SCORPIOIDES M. Sousa ex Cruz Durán & Andrade, **sp. nov**. **TIPO: MÉXICO. Querétaro.** Mpio. Landa: 3.74 km al SSO de San Onofre, 21°12′8.2”N, 99°3′26”W, *E. Martínez* y *C.H. Ramos 41885* (holotipo: MEXU!; isotipos: FCME!, IEB!, MEXU!, MO!). Figura 2.

Lonchocarpo santarosani similis sed foliis cum foliolis minus numerosis, inflorescentiis cum brachyblastis brevioribus sed cum floribus plurimioribus, bracteolis brevioribus et linearibus, et floribus parvioribus differt.

Árboles 2–8 m de alto (rara vez 15–18 m), o arbustos 1–5 m de alto; ramillas y hojas jóvenes con indumento velutino, ferrugíneo a cobrizo; corteza lisa con manchas; corteza interna aparentemente sin exudado resinoso al corte. **Hojas** (11.5–)12–30(–31) cm de largo, con disposición helicoidal; estípulas 1.5 × 1 mm, triangulares, lado externo pubescente; pecíolos (2.2–)3–7.5(–9) cm de largo, teretes, a ligeramente acanalados hacia el ápice, estrigosos; raquis ligeramente acanalado, estrigoso; peciólulos 4–8 mm de largo, pubescentes; folíolos 7–9, rara vez 5, 4–11.5(–12.2) × (1.8–)2–5(–5.8) cm, elípticos a largamente elípticos, opuestos, epunteados, el haz estrigoso sólo en las venas, el envés estrigoso, indumento cobrizo, la base cuneada, el margen revoluto, el ápice agudo; venas secundarias principales 6–7(–9) por lado, venación camptódroma, con venas de quinto grado evidentes. **Inflorescencias** en pseudoracimos axilares, (3.5–)4–7(–10) cm de largo, brácteas, bractéolas y cáliz velutinos, el indumento ferrugíneo a cobrizo; floración coetánea; pedúnculos (2–)2.2–6(–6.5) cm de largo, estrigosos; raquis estrigoso; braquiblastos a modo de cimas escorpioides (5–)8–10 mm de largo, con 4–8 flores; brácteas de braquiblastos 0.7–1 mm de largo, lineares, velutinas, brácteas pedicelares 0.5–0.7 mm de largo, velutinas; pedicelos 2–2.5 mm de largo; bractéolas 0.5–0.6 mm de largo, lineares, velutinas, opuestas, en la base del cáliz, cubriendo una cuarta parte de éste (en flores desarrolladas están en el pedicelo). **Flores** 5–6.5 mm de largo, blancas, blanco con rosa o rosa; cáliz 1.5–2 mm de largo, el diente carinal más largo que el resto; estandarte 5–6 × 4.5–5.3 mm, obovado a orbicular, pelúcido linear-punteado, lámina 4 × 4.5–5.3 mm, pubescente abaxialmente, sin aurículas basales, con callosidades ligeras en la base, uña 1–1.3 mm; alas 5.5–6 × 1.4–1.7 mm, oblongas, pelúcido linear-punteadas, lámina 3.5 × 1.6 mm, pilosa hacia el ápice, uña 1.5–2 mm de largo; pétalos de la quilla 4.8–5.5 × 2–2.1 mm, oblongos, pelúcido linear-punteados, lámina 4.1–5 × 1.8–2 mm, pilosa hacia el ápice, uña 1.5–1.7 mm de largo; androceo 4–5 mm de largo, diadelfo; gineceo 5–6 mm de largo, ovario 3.5–4 mm de largo, velutino, indumento blanco, con 3–4 óvulos, estilo 1–1.5 mm de largo, glabro. **Frutos** (3.1–)3.8–6(–7.6) × 1.5–2 cm, elípticos a oblongos, aplanados, con ala vexilar 1.5–2.5 mm de ancho, tardíamente dehiscentes, estrigosos, base obtusa, ápice obtuso, con 1(–2) semillas. **Semillas** 1.2 × 0.9 cm, reniformes, aplanadas, pardas.

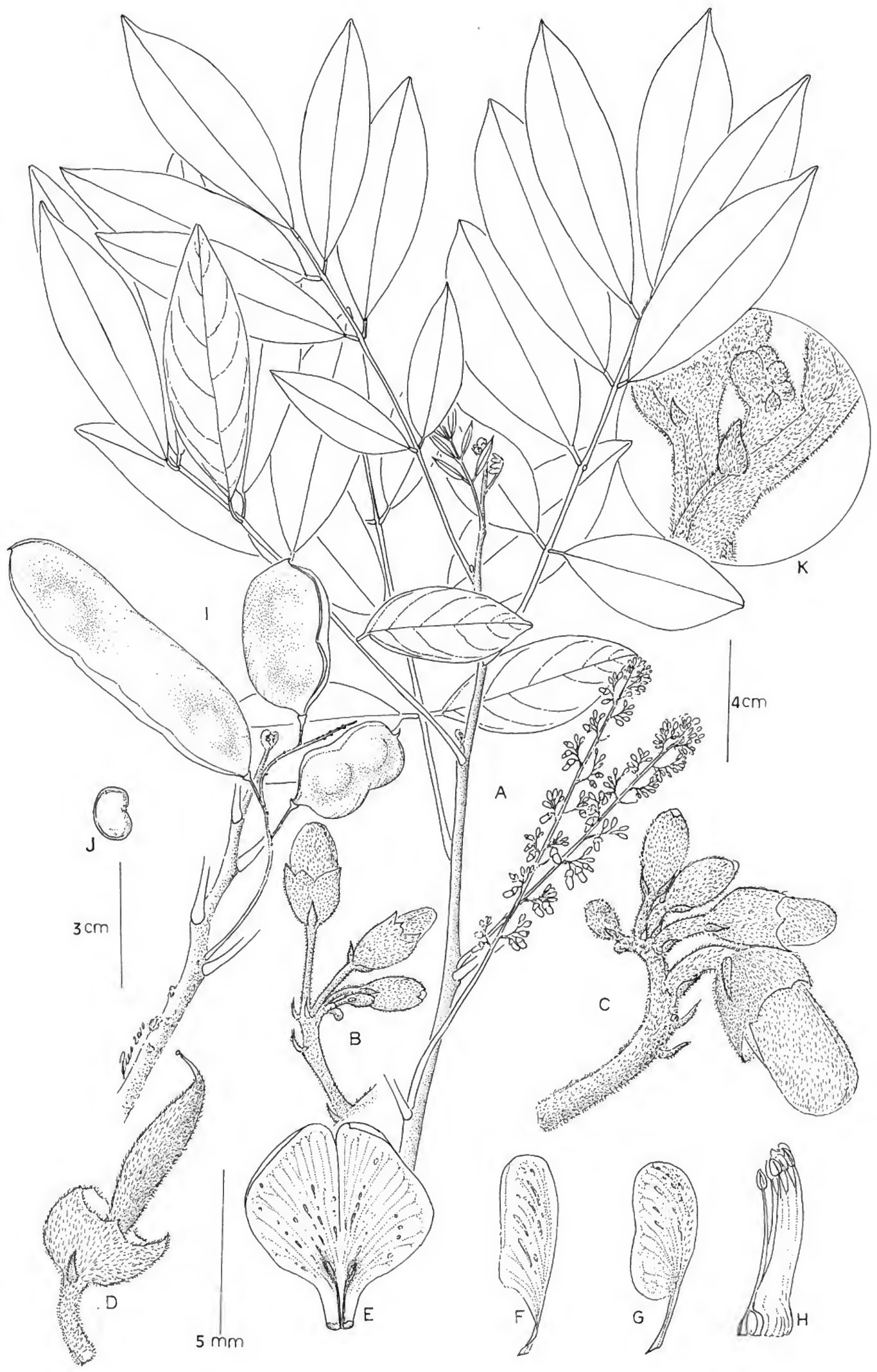

Figura 2. *Lonchocarpus scorpioides*. A. Rama con flores. B. Braquiblasto joven. C. Braquiblasto maduro. D. Cáliz y pistilo, las bractéolas en la base del cáliz. E. Estandarte. F. Ala. G. Pétalo de la quilla. H. Androceo. I. Rama con frutos. J. Semilla, vista lateral. K. Estípula y yema axilar. (A. *Castillo* y *Tapia 642*, MEXU; B-H. *Rubio 1669*, MEXU; I-J. *Tenorio* y *Rubio 19195*, MEXU; K. *Rubio 1669*, MEXU). Ilustración por Ramiro Cruz Durán.

Ejemplares adicionales examinados: **MÉXICO. San Luis Potosí**. Mpio. Huehuetlán: 1 km al NO de Huichihuacan, carretera 85, entre Ciudad Valles y Tamazunchale, *Croat 39231, 39246* (MO). Mpio. Ciudad Valles: Ejido Laguna del Monte, brecha entre Sabinito del Obispo y la mina La Florida, *Fortanelli* et al. *708* (MEXU). Mpio. San Antonio: San Antonio, *Alcorn 338* (MEXU). **Querétaro**. Mpio. Landa: Los Tubos, 2 km al SE, *Rubio 1807* (MEXU); a 3.74 km al SSO de San Onofre, *Martínez* y *Ramos 41911* (FCME, IEB, MEXU); ibid., *Martínez* y *Samain 42500* (FCME, IEB, MEXU); Rancho Nuevo, 2 km al SO de San Onofre, *Rubio 1669*, *1832* (MEXU); 2.5 km al SE de San Onofre, *Rubio 775* (MEXU); al SE de San Onofre, camino Herradura a Rancho Nuevo, *Tenorio* y *Rubio 19195* (FCME, IEB, MEXU); 1 km al O de Camarones, *Rubio 2373* (MEXU). **Hidalgo**. Mpio. Pisaflores: 1 km al E de Pisaflores, *Cartujano* et al. *111* (FCME), ibid., *Cartujano* y *Mayorga 121* (MEXU). **Veracruz**. Mpio. Coatepec: Faldas del cerro Achichuca, entre Tuzamapan y Jalcomulco, Contepec, *Castillo* y *Tapia 642* (ENCB, MEXU, UCAM, WIS, XAL). Mpio. Vega de Alatorre: Cañada de Mesillas, entrada por Santa Ana, *Calzada 7738* (MEXU, XAL); Rancho La Mesilla, camino a Santa Ana, *Calzada 7598* (MEXU, XAL). Mpio. Papantla: 3 km al S de Papantla, *Gómez Pompa* y *González 104* (XAL); El Remolino, *Vargas 148* (XAL). Mpio. Alto Lucero: Carretera Santa Ana-Los Atlixcos, *Vargas 1825* (XAL).

Distribución. *Lonchocarpus scorpioides* se ha localizado en los estados de San Luis Potosí, Querétaro, Hidalgo y Veracruz, en la Sierra Madre Oriental, en aquellos sitios que abarcan lo que se conoce como la Huasteca Mexicana, en altitudes de (20–)150–1000 m, por lo que se espera encontrarlo también en el sur del estado de Tamaulipas y en el norte del estado de Puebla. De esta forma, *Lonchocarpus scorpioides*, al igual que *L. necaxensis*, constituyen casos claros de endemismo en esta región mexicana. Así, la distribución de ambas especies tiene un patrón similar al registrado para *Inga huastecana* M. Sousa (Sousa 1995).

Hábitat. Se encuentra en selva baja caducifolia o subcaducifolia en el ecotono con bosque de *Quercus*, selva mediana subperennifolia, selva baja caducifolia-encinar, bosque de *Quercus*, bosque de *Quercus-Morus*, bosque mesófilo de montaña y selva tropical perennifolia. En suelos negros arcillosos, pardos, con piedras calizas, regosoles y feozem calcáricos. Se encuentra asociada con *Quercus oleoides*, *Cedrela odorata*, *Mirandaceltis monoica*, *Sapindus saponaria*, *Brosimum alicastrum*, *Diospyros oaxacana*, *Fraxinus dubia*, *Lysiloma divaricatum*, *Robinsonella discolor*, *Annona glabra*, *Dalbergia* sp., *Leucaena* sp., y *Cinnamomum* sp.

Fenología. Se ha encontrado en floración de abril a julio y en fructificación de julio a septiembre. Las flores son visitadas por moscas y mariposas.

Nombre común. En el estado de Querétaro se lo conoce como frijolillo.

Afinidades. *Lonchocarpus scorpioides* es similar a *L. santarosanus* Donn. Sm., sin embargo, difiere de este último por presentar hojas con menor número de folíolos, inflorescencias con braquiblastos más cortos, pero con mayor número de flores, bractéolas más cortas y flores más pequeñas. De igual forma, *L. scorpioides* restringe su distribución a la Sierra Madre Oriental en México, mientras que *L. santarosanus* se distribuye desde el Sur de México hasta Guatemala y El Salvador (Cuadro 1).

Cabe señalar que *Lonchocarpus scorpioides* presenta caracteres que la relacionan con el género *Derris* Lour., dentro de la misma tribu Millettieae. Sin embargo, de acuerdo con Sirichamorn et al. (2012), *Derris* es un género con alrededor de 50 especies y estrechamente relacionado con *Lonchocarpus*, *Paraderris* (Miq.) R. Geesink, *Aganope* Miq. y *Ostryocarpus* Hook.f., pero estudios moleculares concluyen que la filogenia de *Derris* s.l. no está resuelta todavía. De igual manera, considerando la morfología de los cinco géneros mencionados, las flores de *Paraderris* son más grandes (más de 10 mm de largo) y usualmente presentan callosidades en la base del estandarte, sus inflorescencias (pseudoracimos) tienen braquiblastos alargados (10–18 mm de largo, como ocurre en *P. montana* (Benth.) Adema) y con 2 o 3 flores en el ápice, en tanto que, en las inflorescencias de *Derris*, los braquiblastos son cortos (como ocurre en *Derris microphylla* (Miq.) Baker, con

braquiblastos de 3–5 mm de largo), en forma de perilla de puerta, aunque en ocasiones también son alargados, con flores distribuidas en toda su longitud, el cáliz es bilabiado (con labio superior 2-lobado y el inferior 3-lobado, como ocurre con *L. scorpioides*), las bractéolas se disponen en el ápice del pedicelo o en la base del cáliz (al igual que en *L. scorpioides*), el estandarte de menos de 10 mm de largo, rara vez con callosidades en la parte basal, estambres monadelfos y legumbres indehiscentes, delgadas, aladas en ambas suturas o sólo en la vexilar. Por su parte, *Aganope* presenta flores en panículas verdaderas (flores solitarias por nudo) y flores con las alas y quilla libres y el androceo diadelfo. *Ostrycarpus* tiene legumbres circulares y nunca aladas. Por último, *Lonchocarpus* generalmente incluye árboles con inflorescencias (pseudoracimos) cuyos braquiblastos generalmente tienen dos flores (y en raros casos 3, aunque ahora en *L. scorpioides* se tienen hasta 8) y frutos usualmente carentes de alas (sin embargo, presentes en *L. scorpioides*), con distribución neotropical, en tanto *Derris* comprende comúnmente lianas (rara vez árboles) con distribución tropical (SE de Asia, África, India, y Sri Lanka); aunque *Lonchocarpus* y *Deguelia* en conjunto se conocen como "*Derris* americano." De igual forma, para Sirichamorn et al. (2014) *Derris* es uno de los géneros más problemáticos en la tribu Millettieae, debido al sobrelapamiento de caracteres con otros géneros como *Aganope*, *Paraderris* y *Solori* Adans. (este último conocido también como *Brachyopterum* (Wright & Arn.) Benth.), sin embargo, *Derris* presenta dos sinapomorfias: hábito de liana (generalmente) y legumbres con alas en ambos márgenes. También señalan que, además de pseudoracimos, el género puede presentar panículas verdaderas. Así, *Lonchocarpus* presenta árboles con distribución neotropical, frutos usualmente carentes de alas, estambres diadelfos o pseudomonadelfos y pseudoracimos con braquiblastos que generalmente presentan dos flores.

Al igual que *Lonchocarpus necaxensis, L. scorpioides* pertenece a la sect. *Densiflori* Benth. que, de acuerdo con Sousa (2005), se caracteriza por presentar el tallo y ramas con corteza interior sin exudado resinoso al corte, folíolos generalmente con el ápice acuminado a agudo, en ocasiones obtuso, venación foliar camptódroma, estípulas, brácteas y bractéolas lanceoladas a linear-lanceoladas u oblongas, siempre más largas que anchas, bractéolas alternas a subopuestas, generalmente distantes del cáliz (como ocurre con *L. necaxensis* y *L. scorpioides*, en flores ya desarrolladas), cáliz lobado, ovario con (1–)2–4(–5) óvulos, legumbres indehiscentes, con el margen vexilar aquillado a alado, en ocasiones ligeramente sulcado (sin embargo, en *L. necaxensis* y *L. scorpioides* el fruto es tardíamente dehiscente por el margen vexilar) y plántulas con los cotiledones hipogeos y eofilos opuestos, unifoliolados.

Cuadro 1. Comparación de caracteres de *L. scorpioides* y *L. santarosanus*

Caracteres	***L. scorpioides***	***L. santarosanus***
Folíolos, número	(5–)7–9	(11–)13(–15)
Braquiblastos, longitud	(5–)8–10 mm	hasta 14 mm
Flores, número por braquiblasto	4–8	2–3
Bractéolas, longitud, forma	0.5–0.6 mm, lineares	0.8–1 mm, triangulares
Flores, longitud	5–6.5 mm	7–9 mm
Distribución	Sierra Madre Oriental, México	Sur de México hasta Guatemala y El Salvador

Etimología. El nombre de la especie hace alusión a la apariencia de cimas escorpioides, que tienen los braquiblastos de los pseudoracimos, como lo señalara, en su momento, Mario Sousa Sánchez.

Apéndice 1

Ejemplares de *Lonchocarpus santarosanus* y *Derris microphylla* utilizados en la comparación con *L. scorpioides*

Lonchocarpus santarosanus Donn. Sm. **MÉXICO**. **Tabasco**. Mpio. Teapa: balneario Puyacatengo, 12 nov 1984 (flor), *Sousa* et al. *12797* (XAL). **Veracruz**. Mpio. Chicomapa: 10 nov 1976 (flor), *Vázquez* 549 (XAL). Mpio. San Andrés Tuxtla: por la orilla del camino a la playa, 0.5 km desde Balzapote, 8 nov 1978 (flor, fruto), *Shapiro 202* (XAL). Mpio. Playa Vicente: El Nigromante, 15 oct 1971 (flor), *Chavelas* et al. *ES–4314* (XAL).

Derris microphylla (Miq.) Valeton ex Baker **MADAGASCAR**. **Fianarantsoa Province**. National road 25 between Ifanadiana and Kianjavato, 23.5 km E of Ifanadiana, *Turk 590* (MEXU). Especie cultivada.

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SYSTEMATICS, EVOLUTION, AND PHYLOGEOGRAPHY OF MONTIACEAE (PORTULACINEAE)

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ABSTRACT

Montiaceae (Portulacineae) comprise a clade of at least 268 species plus ca. 27 subspecific taxa primarily of western North America, the Chilean Floristic Region, and temperate Australasia. This work uses existing phylogenetic metadata to elaborate a new cladistic taxonomic synthesis. A total of 24 taxa are validated, nine new and 15 necessary nomenclatural recombinations. Hypotheses of Montiaceae historical, biogeographical, ecological, and phenotypic evolution are evaluated in light of recent metadata and in terms of classical, contemporary, and novel systematic and evolutionary epistemology.

This work presents a new cladistic taxonomy of Montiaceae (Portulacineae) and a review of their phylogeny and ecological, phenotypic, and biogeographic evolution. Considerable emphasis is placed on theory and epistemology. The work partially is a redrafting of Hershkovitz (2018a) but is highly modified and corrected and includes significant changes from previously circulated preprints under the this title. The taxonomy includes 24 nomenclatural novelties. The generic circumscriptions and diversity estimates are modified from Hernández-Ledesma et al. (2015). The suprageneric taxonomy is the first proposed since McNeill (1974) and the only phylogenetic one.

This work first summarizes evidence for diversity, phylogeny, ecological, phenotypic, and biographical evolution of Montiaceae. The taxonomy follows. The generic taxonomy supersedes that of Hernández-Ledesma et al. (2015), which superseded that of Carolin (1993) and Hershkovitz (1993a). In addition, I comment on the taxonomy and taxonomic history of selected taxa, especially *Calandrinia* Kunth, *Rumicastrum*, and *Cistanthe* Spach, and recombine binomials into *Cistanthe*, *Calyptridium* Nuttall and *Philippiamra* Kuntze, and erect a new genus, *Thingia* Hershk. I also conclude that *Lewisiopsis* Govaerts has a hybrid origin and represents a living fossil.

2. Montiaceae Species-Level Diversity

The present synthesis conceives of Montiaceae as comprising ca. 268 species plus ca. 27 additional subspecific taxa, thus ca. 292 (sub-)specific taxa in total. These figures seem substantially higher than the "about 200" species estimated by Hernández-Ledesma et al. (2015). Much of the difference owes to a near doubling of the estimate of species diversity in the Australian genus *Rumicastrum* over the past two decades (Hancock et al. 2018). New species discovery among American taxa has been much less. In these, the modest increase in species diversity estimates owe mainly to additional study of known species, resulting in taxonomic segregation of previously studied and classified individuals and populations.

The estimate of (sub-)species diversity begs the question of the ontological nature of species and the criteria used to diagnose them. Aperture of this Pandora's Box is beyond the scope of this work, but it should not be ignored, either (McDade 1995). Perhaps it is better to emphasize that species diversity estimates and taxonomies applied in this work are *not* intended to reflect the criteria of any of the 30 or so proposed species concepts (Hey 2006), e.g., biological species or phylogenetic species or any other species of "species." This introduces no taxonomic controversy here, because, in general, such criteria have not been applied explicitly in developing Montiaceae species taxonomy.

The species diversity estimates and taxonomies applied here derive from subjective seat-of-the-pants typological classification, whereby the arbiters of (sub-)species are type specimens. (Sub-) species thus comprise real or hypothetical individuals considered to be conspecific with type specimens and, perhaps more importantly, to no *other* named or unnamed (sub-)species. It should be emphasized, in this regard, that there is nor shortage of accepted presumed taxa known only from single individuals, e.g., the genus *Schreiteria* among Montiaceae. The present work defers to the experience and "authority" of multiple contemporary and past students of Montiaceae (sub-)species taxonomy, including myself as appropriate.

Most of this taxonomy is based mainly on intuitive interpretation of morphological variability and geography, in a relatively few cases incorporating also cytological and genetic evidence. Not surprisingly, genetic and/or statistical evidence has been applied to species discrimination mainly for certain North American Montiaceae, in particular species of *Calyptridium* (e.g., Simpson et al. 2010), *Claytonia* (e.g., Stoughton et al. 2017a, b), and *Lewisia* (Foster et al. 1997). But especially for southern hemisphere Montiaceae, species discrimination derives mainly from subjective morphological and geographical studies, historically mainly by northern hemisphere botanists, but that is changing. Cytological criteria have been used mainly in *Claytonia* (Miller & Chambers 2006) but also in some *Phemeranthus* spp. (Price 2012).

Stoughton et al. (2017b) claimed to apply the "unified species concept" (De Queiroz 2005) for *Claytonia*. However, the unified species concept and its contemporary companion buzz term "integrative taxonomy" (e.g., Dayrat 2005) amount to old wine in new bottles. These concepts advocate pluralistic "total evidence" approaches to taxon discrimination. But, other than incorporating modern genetic and/or statistical approaches, they otherwise are indistinguishable from 18th century subjective typological taxonomy. No particular objective criterion is applied consistently and/or uniformly. Even under this epistemologically permissive concept, Stoughton et al. (2017a) demonstrated that about 10% of sampled individuals of the *Claytonia lanceolata* Pursh complex could not be classified and that the number of unclassifiable individuals was the same as the number of recognized species (discussed later).

Montiaceae species as conceived here and historically are references for taxonomic/ biogeographical *diagnosis/description* only, and for filing specimens in herbaria. Most importantly, the species, their reported essential and/or diagnostic traits, and their incumbent trait variation do *not* represent independent and identically distributed observations for purposes of statistical biogeographical or evolutionary analysis. Such analyses presume that species and their traits are tangible entities so distributed. The failure of taxonomic species to conform to this presumption (empirically or epistemologically) undermines or invalidates much of quantitative evolutionary analysis, as discussed later.

Moreover, unappreciated is the fact that operational species technically are diagnosed not on the basis of what they *are*, but, rather, what they are *not*. Technically, what species *are* is *not other* species. This reflects the nomenclatural convention that mandates that every *new* species must be, in principle, not more or less than diagnostically different from *existing* species. Thus, ontologically, species are singularities, unique forms of life. Their uniqueness means that they are not permutations of other forms or draws from a linear distribution (see also below). The onus is on the statistical analyst to demonstrate the statistical properties of analyzed taxa.

One means of skirting the species concept issue might be to apply the term "specioid." This term has been proposed to refer to cultivated plant varieties that are not taxonomic species but share the ontological properties of being recognizable in one or another dimension and named as distinct entities for communication purposes (Jirásck 1964). Thus, the term specioid can be used to also to refer to a species defined by any operational criterion, however arbitrary, completely agnostic towards

the nature of species. Montiaceae can be described taxonomically as having ca. 300 morphologically/ geographically distinguishable specioids, or taxonomic reference points (species and subspecific taxa). Parochial species concepts might yield qualitatively/quantitatively different specioids. At the same time, quantitative biogeographic/evolutionary research can emphasize analysis of specioids whose ontology is transcendental and whose taxonomic designations are for reference purposes only. In other words, no particular species circumscription/taxonomy need be implied. The only requisite is the evidential correspondence of analyzed individuals to the types of the named species. In this case, statistical properties, valid or not, can be ascribed to specioids.

As in all taxonomic groups, some Montiaceae species identities/circumscriptions seem clear and uncontroversial, while others are ambiguous. And some taxa have been studied more thoroughly than others. *Lewisia* is a genus that has been relatively well-studied taxonomically compared to certain other Montiaceae (Hershkovitz & Hogan 2002, 2003). Four comprehensive treatments have been published since 1966, as well as several more floristic treatments that include several to most species, especially those covering California. Yet, no two treatments are exactly alike, and even Hershkovitz & Hogan (2002, 2003) noted the inadequacy of their own treatment, especially with respect to the *L. pygmaea* (A. Gray) B.L. Rob. complex (see later discussion). At the other extreme, there is no critical comprehensive taxonomic treatment of *Cistanthe* sensu Hershkovitz (2006). The treatment that is most recent and comprehensive is Reiche (1898), which covers only the Chilean species.

In a privately-circulated, unpublished manuscript, I attempted to resolve not the ontology of species but the intransigence of individuals to sort themselves into taxa. I described a dynamical process of diversification called the "wave model" that predicts variable degrees of instantaneous species discreteness. Using analogies to wavescape features, especially dynamism, complexity, fractal qualities, and the axiom that, instantaneously, not all water pertains to waves, this model, as opposed to a species concept, attempted to describe biodiversity more objectively and without preconceived notions of what species are or ought to be or how they form.

The wave model was inspired by field observations of Atacama Desert Montiaceae. Here, because of low competition and little ecological community structure/stability, the emergence of a specioid entity is mainly a function of chance survival and proliferation of a novel and *viable*, as opposed to *optimal*, form in *transitionally* adequate conditions. In particular, a novel form must occur in a location that permits nothing more than growth and reproduction, without otherwise being more "adapted" than its progenitors. Other organisms are scarce in patches of barren desert, so infraspecific/interspecific biotic interactions have less impact, positive or negative, on survival. The limiting factor is mainly water, in particular its spatiotemporally irregular distribution. And evidently seeds of desert Montiaceae can survive decades without water. Thus, with few growth/reproductive episodes, a novel form can survive for centuries, even millennia.

At some point, change in conditions might permit greater proliferation of the novel form, so that its perceptual status changes from that of an odd mutant to a taxon. A wave. This may owe to changing conditions locally, or the novel form might disperse to different location. The model is applicable to all ecological conditions, not just the desert. Spatiotemporal separation of organisms and generations in the desert simply render it more apparent. The model is corroborated by phylogenomic studies like that of Stoughton et al. (2017a). In particular, in some timeframe prior or posterior to the present – *or* under slightly different historical circumstances – the singular unclassifiable forms might have proliferated and the proliferated classified forms vice versa (see also later discussion of phylogenomics).

Hershkovitz (2006) noted that phylogenetic trees derived using standard species-level phylogenetic markers exhibited long branches subtending several Montiaceae genera and very short,

irresolvable interspecific branches (cf. Ogburn & Edwards 2015). This was despite ample morphological and ecological divergence and diversity, e.g., between diminutive, tiny-flowered annual versus suffruticose, large-flowered species, distributed in habitats ranging from sea-level to over 4000 m and hyperarid to subaquatic. Similar lack of interspecific phylogenetic resolution later was found in *Phemeranthus*, the "oldest" genus of the family (Price 2012).

These molecular data suggest recent and rapid species radiation, but Hershkovitz (2006) mused whether the low genetic divergence reflected hybridization. Lineage sorting emerges as another possible cause (Copetti et al. 2017; Stoughton et al. 2017a). Regardless, Hershkovitz (2006) speculated that genomic and phenomic evolution were decoupled, such that the considerable phenotypic diversification actually occurred over a longer period, whereas the sampled DNA loci "surfed" the evolving species without themselves proportionally diverging/diversifying. Both hybridization and lineage sorting could yield such an effect.

3. Montiaceae Phylogeny

3a. Relations of Montiaceae and Portulacineae. Formerly, Montiaceae were included in the traditional but paraphyletic family Portulacaceae (Nyffeler & Eggli 2010a). Its conceptual origins trace to Hershkovitz (1993a), who referred to a group denominated Western American Portulacaceae, members of the family diversified primarily westwards of the American cordillera. Molecular analysis (Hershkovitz & Zimmer 1997) showed that Western American Portulacaceae comprised most of a clade they called the PAW clade, comprising: *Phemeranthus* Raf., the Australian genus *Rumicastrum* Ulbrich, and the taxa included in Western American Portulacaceae. The current circumscription of Montiaceae corresponds to the PAW clade and was completed with the addition of Hectorelleae (Applequist et al. 2006; Wagstaff & Hennion 2007).

The modern cladistic generic classification of Montiaceae originated with morphological analyses by Carolin (1987, 1993) and Hershkovitz (1991a, 1993a). Slowly, the new familial and generic concepts began to replace the traditional generic concepts of Pax & Hoffmann (1934) and McNeill (1974). Molecular evidence, beginning with Hershkovitz & Zimmer (1997), stimulated further acceptance of the cladistic classification and fomented several subsequent studies. Here I elaborate a modified cladistic supraspecific taxonomy based on molecular evidence, especially Hershkovitz (2006), Ogburn & Edwards (2015), Hancock et al. (2018), and Goolsby et al. (2018a, b). Most of this evidence was reviewed in Hershkovitz (2018b), which is undergoing revision.

Current targeted-gene phylogenetic and phylogenomic evidence (Ogburn & Edwards 2015; Smith et al. 2017; Goolsby et al. 2018a, b; Hancock et al. 2018; Wang et al. 2018; Yang et al. 2018; Marinho et al. 2019) places Montiaceae as sister to remaining Portulacineae. The latter comprises six families, including several genera of classical Portulacaceae and the classically segregated families Basellaceae, Cactaceae, Didiereaceae, and Halophytaceae. Most analyses place Portulacineae, in turn, as sister to Molluginaceae as currently circumscribed (Hernández-Ledesma et al. 2015; Ogburn & Edwards 2015; Smith et al. 2017; Hancock et al. 2018; Wang et al. 2018). However, one phylogenomic analysis found lower support for this relationship "than predicted" (Moore et al. 2017). Possibly the discrepancy is moot, given the high divergence between Portulacineae and Molluginaceae and, for that matter, any other candidate outgroup .

Consensus on the generalized phylogenetic position of Portulacineae is not absolute, however. Based on anatomy/morphology, Wang (2018) advocates a radically contrasting view of Caryophyllales and Portulacineae relations. Caryophyllales "should be among the most primitive of angiosperm groups" (Wang 2018: 352). This interpretation resurrects several unorthodox morphological interpretations proposed during the late-19th to mid-20th century. Citing reproductive traits *especially* of certain Portulacineae, Wang (2018) has proposed that Portulacineae are derived from Cordaitales, a Carboniferous seed plant lineage.

Wang (2018) does not reconcile his view with ever-accumulating genomic evidence that "core" Caryophyllales comprise the terminal clades of a broader and remarkably diverse Caryophyllales "sensu lato," well-nested within eudicots. Although the consensus position of Caryophyllales has migrated somewhat over the past two decades with increasing gene/taxon sampling, current analyses (Angiosperm Phylogeny Working Group 2016) position Caryophyllales sensu lato as sister to asterids, the most "advanced" of angiosperms. Inadequacy of the fossil record duly noted, Wang (2018) does not address the apparent paradox that existing stratigraphic *sequences* correlate well with phylogenetic evidence. To be fair, however, Wang (2018 and cited references) indeed argues that many pre-Cretaceous fossils are angiospermous. Thus, evidently he does believe that Portulacineae and dinosaur footprints, perhaps along with human, eventually might be found side-by-side.

Another conflicting interpretation of Portulacineae relations is presented by Liu et al. (2018). Their phylogenetic analysis of 48 protein-coding chloroplast genes from 35 Caryophyllales (sensu lato) species yielded what can only be described as a "random" – yet highly statistically supported – phylogeny. None of the familial/ordinal level phylogenetic structure of the consensus phylogeny is evident. Samples of multiply-sampled genera, such as *Silene*, *Fagopyrum*, *Salicornia*, and *Drosera* intersperse throughout the tree. The four samples of Portulacineae genera (*Carnegia*, *Cistanthe*, *Portulaca*, and *Talinum*) do also. I make no attempt here to reconcile or explain the results of Liu et al. (2018).

In retrospect, the cladistic position of Montiaceae among Portulacineae might seem unexpected. Compared to the clade comprising remaining Portulacineae, Montiaceae are less diverse morphologically, genetically, and taxonomically (comprising about 15% of Portulacineae species diversity). Moreover, their "centers of diversity" developed geologically relatively recently: mountainous and arid regions of temperate western America. Remaining Portulacineae have a more tropical Gondwanan distribution (discussed below). Molluginaceae are mainly African.

On the basis of morphology, my initial expectation was that Montiaceae would prove to be nested "within" a much older Portulacineae, more or less as indicated in Carolin (1987). This expectation owed to the morphological similarity and biogeographic proximity of herbaceous perennial species of *Talinum* with many species of the grade group *Calandrinia* sensu lato (discussed below). Indeed, these taxa classically had been classified in the same tribe (Pax & Hoffman 1934; McNeill 1974), and historically, species of one genus variously had been described and/or classified as species of the other (discussed below). Furthermore, *Phemeranthus* had been included in *Talinum* by all authors since 1828, and its current segregation was resisted for more than a decade following the cladistic conclusions of Carolin (1987). Thus, the intergradations between *Talinum* sensu lato and *Calandrinia* sensu lato, along with geologically recently developed habitats of the latter, suggested nesting of Montiaceae within classical Portulacaceae.

Interestingly, the earlier morphological cladistic analysis of Hershkovitz (1993a) was more or less consistent with Montiaceae being the sister of remaining Portulacineae, even though no particular outgroup was specified. That work noted that "the cladistics results suggest that the western American group [i.e., Montiaceae] is as old as if not older than the eastern American/African group [i.e., remaining Portulacineae]" (Hershkovitz 1993a: 350–351). It also pointed out that presumably "primitive" tricolpate pollen was widespread among (effective) Montiaceae, whereas among classical Portulacaceae, it was restricted otherwise to *Portulacaria* and *Ceraria* (Didiereaceae). The latter, it turns out, belong to the lineage diverging after Montiaceae. Hershkovitz (1991b, 1993a) also argued that Cactaceae seemed to nest between *Talinum* and a clade of taxa sharing chromosome base number 9, *Portulaca* and the Anacampseroid genera.

The first relevant molecular analysis, based on nuclear ribosomal internal transcribed spacer (ITS) sequences (Hershkovitz & Zimmer 1997), was not far off from the current phylogenetic consensus for Portulacineae. The midpoint-rooted tree showed Basellaceae/Didiereaceae (as currently circumscribed) as sister to remaining Portulacineae, with Montiaceae diverging subsequentially. This appears to be a branch length artifact, i.e., the midpoint occurred along the especially long branch of Basellaceae/Didiereaceae. But no basis for outgroup rooting existed at that time. Re-rooting the midpoint-rooted tree one node up would generate the current view. Hershkovitz and Zimmer (1997) also corroborated the morphologically-based conclusions regarding the position of Cactaceae.

Current molecular/genomic evidence for Portulacineae relations ought to instill appreciation for the morphological cladistic analyses of Carolin (1987) and Hershkovitz (1993a). Carolin's (1987) work was seminal and radically transformed phylogenetic concepts pervasive up to the end of the 20th century. Up until then, phylogenetic studies proceeded taxonomically top-down, using existing classical higher-level taxa as taxonomic units (e.g., Rodman et al. 1984; Rodman 1990; cf. Hershkovitz 1989; see also chapters in Behnke & Mabry 1994). This presumed that higher-level taxa were monophyletic, a notion which Rodman (1990) defended. The first molecular phylogenetic analyses of the order also proceeded top-down (Rettig et al. 1992; Downie & Palmer 1994; Manhart & Rettig 1994). Because these studies sampled classical families sparsely, they failed to discover familial paraphyly/polyphyly.

Carolin's (1987) approach was bottom-up, seeking to discover clades among Portulacineae based on character evidence and not taxonomic prejudice. Hershkovitz' (1993a and cited references) effort began independently of Carolin's and came to similar, but not identical, conclusions. Both works represent the first and only detailed bottom-up computational morphological cladistic analyses of a Caryophyllales family. Hershkovitz (1993a) was the first and only to consider explicitly and analytically the paraphyly of a Caryophyllales family.

By 1993, the phylogenetic paradigm shifted abruptly and decidedly from morphology to molecular. Hershkovitz (1993a) provided the hypothetical template for Hershkovitz & Zimmer (1997, 2000) and subsequent molecular and genomic phylogenetic (and phylogeographic and evolutionary) analyses of Portulacineae. Hershkovitz and Zimmer (1997, 2000) corroborated several ideas of Hershkovitz (1993a), including some but not all novel generic circumscriptions and the relations of Basellaceae, Cactaceae, and Didiereaceae. Hershkovitz and Zimmer's (1997) study overcame numerous technical and analytical challenges, as described therein.

But just after that point, technological and analytical advances rendered molecular phylogenetics more an endeavor of "acquisition" than "inquisition." In particular, advance depended not so much on knowledge, theory, and problem-solving than it did on the acquisition of unsampled taxa and the wherewithal to run them through the largely automated laboratory and computational mill. To paraphrase James Watson, "any monkey could have done it." In some cases, e.g., Liu et al. (2018), a monkey could not have done it any worse.

However, when it emerged, the Carolin/Hershkovitz phylogenetic framework was not embraced widely. This is evident partially in the long delay in nomenclatural transfer of species into their currently accepted genera, as discussed later. This delay continues to the present day in the case of *Rumicastrum* species, still incorrectly classified in *Calandrinia* sensu lato more than three decades after Carolin's work (e.g., Goolsby et al 2018a, b; Hancock et al. 2018; see also the taxonomic section below).

Prolonged skepticism towards the conclusions especially of Hershkovitz (1993a) is evident also in Cuenod et al. (2002), who intimated that paraphyly of Caryophyllales families was their own

discovery, *especially* nesting of Cactaceae among classical Portulacaceae (see Kew Scientist 2001). At the minimum, the intimation demonstrates that, despite the morphological and molecular evidence advanced by Hershkovitz (1989, 1991a–d, 1993a; Hershkovitz & Zimmer 1997), Cuenod et al. (2002) did not *anticipate* paraphyly of Caryophyllales families. Possibly this was true more broadly in the plant systematics community (but see Brummitt 2002). Other researchers (e.g., Moreira Muñoz 2011) evidently did not appreciate that currently conceived Cactaceae relations were resolved well before their molecular-based corroboration (Hershkovitz 1991b, 1993a) and that similarities between Cactaceae and certain classical Portulacaceae had been noted by multiple researchers since the 19th century (Hershkovitz 1993a; Metzling & Kiesling 2008).

3b. Relations among Montiaceae. With caveats, current molecular phylogenetic evidence suggests the following sequence of divergences and intergeneric-level relations (Ogburn & Edwards 2015: Fig. 2; Hancock et al. 2018: Figs. 3–4; cf. Hershkovitz 2018b).

1. *Phemeranthus* as the outgroup of the remainder of Montiaceae. This accords with morphological and phylogeographic evidence. On morphological bases (elaborated later), I here classify *Phemeranthus* and *Schreiteria* in Phemerantheae.

2. Divergence/diversification of a clade here denominated Cistantheae, a principally Chilean (semi-) arid region lineage that includes: (a) *Cistanthe*; (b) *Montiopsis*; and (c) Calyptridinae, comprising *Lenzia*, *Calyptridium*, *Philippiamra* and *Thingia*.

3. Concomitantly, paraphyly of *Cistanthe* sensu Hershkovitz (1991a, 1993a; cf. Hershkovitz 2006; Ogburn & Edwards 2015). However, Hershkovitz (2018b) argues that morphological similarities shared by members of *Cistanthe* sensu Hershkovitz (1993a) may be symplesiomorphies, historical synapomorphies lost in more recently divergent lineages.

4. Divergence of *Rumicastrum*. Hershkovitz (2018a) included this genus in Montioideae (see below), but ecological divergence compels me to leave it isolated, thus separating Montiaceae into a *grade* of primarily ancestrally warm/arid-adapted succulents ("paleomonts") from a clade of decidedly more cool/moist-adapted Montioideae.

5. Monophyly, hence, of a clade here denominated Montioideae, comprising remaining Montiaceae.

6. Divergence of *Calandrinia*, although one of the 12 data/method combinations in Hancock et al. (2018) yielded maximal support for a conflicting topology, in which *Calandrinia* is sister to Cistantheae.

7. Divergence of Hectorelleae. Support for this relation degenerates markedly in the five- compared to the three-marker data in Ogburn & Edwards (2015), but no Hectorelleae data were available for the additional two markers, which are more rapidly-evolving (Hershkovitz 2018b). This suggests that the inclusion of more rapidly-evolving markers introduced not conflict, but noise that perturbed the statistical support.

8. Divergence/diversification of a clade here denominated Montieae, a principally western North American lineage including *Lewisiopsis*, *Lewisia*, *Claytonia*, and *Montia*.

9. A hybrid origin of *Lewisiopsis* (see Hershkovitz 2018a, b; see also below). This hypothesis is supported by strong conflict of *Lewisiopsis* sister relations based on plastome and nucleosome data. The former support a sister relation with *Lewisia*; the latter with a clade comprising *Lewisia* and Montiinae. In addition, the root-to-terminal *Lewisiopsis* branch length is exceptionally short in phylograms in all molecular/genome analyses, from Hershkovitz & Zimmer (1997) to Goolsby et al. (2018a, b). The patristic distance between *Lewisiopsis* and *Cistanthe* is about the same as or

generally less than that between *Lewisiopsis* and other Montieae. This parallels the morphological data (Hershkovitz 1992). The evidence suggests that *Lewisiopsis*, in conjunction with its hybrid origin, has persisted as a "living fossil" that has retained genomic and phenotypic characteristics of a *Cistanthe*-like ancestor.

10. The uncontroversial sister relation of *Claytonia* and *Montia* (but see trees in Marinho et al. 2019), often classified as Montieae, but here classified as Montiinae.

In addition, existing evidence supports several infrageneric-level phylogenetic relations:

1. Monophyly of two subclades of *Phemeranthus*, one comprising the (sub-)caulescent species, the other the acaulescent (Price 2012).

2. Monophyly of *Cistanthe* sections *Cistanthe* and *Rosulatae*, each including annual and perennial species.

3. Despite poor overall resolution, monophyly of two subclades within *Cistanthe* sect. *Rosulatae*, each of which is polymorphic for life history. These subclades are recognized as subsections here and in Hershkovitz (2018a). Otherwise, genetic divergence is too low to resolve interspecific phylogenetic relations (Hershkovitz 2006).

4. Possible paraphyly of *Calyptridium* sect. *Calyptridium* with respect to *C.* sect. *Spraguea*. The latter includes the only perennial species of the genus.

5. Tentatively, monophyly of both the perennial and annual clades of *Calandrinia* (Hershkovitz 2006; Ogburn & Edwards 2015), which is not supported mutually by independent phenotypic traits (Hershkovitz 1993a). However, Goolsby et al.'s (2018a, b) phylogenomic analyses show paraphyly of the annual *C.* sect. *Calandrinia* with respect to the perennial *C.* sect. *Caespitosae* (syn. *C.* sect. *Acaules*; see taxonomic section below). This result is problematic (see below), but is not otherwise implausible. Hershkovitz (1993a) suggested the contrary relationship, *C.* sect. *Caespitosae* paraphyletic with respect to *C.* sect. *Calandrinia*, evidenced by morphologically intermediate traits of the annual *C. nitida* (Ruiz and Pav.) DC (synonym: *C. axilliflora* Barnéoud). Interestingly, Goolsby et al.'s (2018a, b) analysis shows *C. nitida* as sister to the perennial clade. If correct, Goolsby et al.'s (2018a, b) results provide another example of a transition from annual to perennial life history, as Hershkovitz (2018c; *contra* Carolin 1987, Hershkovitz 1993; Ogburn & Edwards 2015) argued was the predominant polarity among Montiaceae (see also below).

6. Monophyly of the perennial *Montiopsis* subg. *Dianthoideae*, which lack a phenotypic synapomorphy (Hershkovitz 1993a). Genetic divergence among the annual and perennial species of *M.* subg. *Montiopsis* is insufficient to resolve their phylogenetic relations (Hershkovitz 2006).

7. Somewhat ambiguous support for monophyly of two principal groups of *Lewisia*, one comprising the "evergreen" species (*Lewisia* sect. *Cotyledon*; Mathew 1989). Leaves of these species are coriaceous and persist year to year. In agreement with my unpublished data, the section is monophyletic in Goolsby et al. (2018a, b) with the exception of *L. congdonii* (Rydb.) S. Clay. The latter species shares reproductive morphology of the evergreen species, but has ephemeral leaves (Mathew 1989). The known interfertility among many *Lewisia* species (Mathew 1989; Davidson 2000) raises the possibility that *L. congdonii* has a hybrid origin. Resolution is poor among remaining species of the other subclade, which are morphologically diverse but share ephemerality of their leaves.

8. Monophyly of three *Claytonia* sections differing in life form/history: annual, rhizomatous perennial, and caudiciform taproot or tuberous (O'Quinn et al. 2005). Again, this seems to rule out paraphyly of perennials with respect to annuals, rendering less certain evolutionary polarities.

9. Monophyly of three clades within *Montia* (O'Quinn et al. 2005).

Although it may seem trivial to point out, monophyly described above (and in general) refers to existing evidence supporting monophyly of extant clade members. This does not imply necessarily that the phenotypic differences between the clades originated in a single common ancestor or ancestral species that split into two. Gene trees, species trees, and phenotypic trait trees are presumed to be colinear, but they are not the same. Phenotypic synapomorphies can originate before or after molecular marker synapomorphies, and also via lateral transfer. Whole genome analyses (see below) just now are scratching the surface of the complexity underlying phylogenies artificially simplified by analysis of few genetic markers. Thus, the sense of monophyly applied in this work and more broadly in contemporary systematics is simplistic and may be naïve.

3c. Phylogenomic evidence for Montiaceae phylogeny. Within the past few years, now "classical" targeted-gene molecular phylogenetics has ceded significantly to phylogenomics, phylogenetic analysis of thousands of relatively short (> 300 bp) sequence fragments sampled from whole genome DNA or transcriptomes. Using computer programs, the short fragments often are assembled into longer contiguous fragments. Within the past two years, eight phylogenomic analyses have been published that include significant Montiaceae data (Moore et al. 2017; Smith et al. 2017; Stoughton et al. 2017a; Yang et al. 2017; Goolsby et al. 2018a, b; Hancock et al. 2018; Walker et al. 2018; Wang et al. 2018). In some cases, phylogenomic studies are a hybrid between phylogenetics and functional genomics, i.e., emphasize genomic sampling for particular functional genes (e.g., Goolsby et al. 2018). A deluge of phylogenomic data is likely to appear in coming weeks and months.

Phylogenomic analysis currently presents numerous technical, analytical, and epistemological challenges that will be reviewed in greater detail in a revision of Hershkovitz (2018b). One challenge is common to all phylogenetic and, in fact, evolutionary analysis in general. In particular, statistical analyses obligate the assumption that observed data are generated according to models used to reconstruct their evolutionary history. Yet, models are approximations and "are never true in real data analysis" (Yang & Zhu 2018: *1854*; cf. Gunawardena 2014). But phylogenomics adds additional challenges.

1. Genome-level evolutionary models are more precarious. Model violations are somewhat tractable in analysis of modest-length, well-studied, and broadly sampled phylogenetic markers. Even then, models usually falsely assume molecular evolutionary stationarity across phylogenetic sample space (Hershkovitz 2018b). Model violations are (practically) intractable in the analysis of hundreds to thousands of machine-sampled, machine-assembled DNA fragments summing to more than 100,000 nucleotide base pairs.

2. Phylogenomic analyses generally emphasize multi-species coalescent model reconstruction, which introduces dicey assumptions on lineage effective population size and generation times during diversification over the course of tens of millions of years (Xu & Yang 2016).

3. The size of phylogenomic data sets constrains their analysis to less rigorous "summary methods" (Xu & Yang 2016) and/or problematic Bayesian methods (Yang & Zhu 2018).

4. If applicable, sampling bias for particular functional genes introduces the specter of convergence in phylogenetic analysis.

The analytical and interpretive challenges do not mean that phylogenomic reconstructions are "wrong." In fact, most nodes emerging from phylogenomic analyses seem to corroborate those of targeted-gene phylogenetic estimates. But not always, e.g., in the case of Molluginaceae-Portulacineae monophyly (Yang et al. 2018) and relations within *Calandrinia* (Goolsby, et al. 2018a, b). Such discrepancies can be understood intuitively. A determination that a racehorse can run faster than a turtle may not be especially sensitive to experimental or analytical method or assumptions or measurement error. But determining which was the fastest racehorse ever, if that is possible, is another matter. Here we expect assumption/data sensitivity and, in empirical Bayesian estimation, maximal support for incorrect and conflicting conclusions. But the analytical intractability of phylogenomic data creates an additional epistemological dilemma. Should we incline towards phylogenomic conclusions, because more data is better? Or should we accept that phylogenomic conclusions are generated by machines and remain, at this point, outside of the realm of human intellectual scrutiny and sensibilities?

An illustrative example of the challenge of phylogenomics emerges in the analysis of the *Claytonia lanceolata* complex (Stoughton et al. 2017a). Without doubt, the approach yielded significant discoveries facilitating the recognition of distinct evolutionary lineages in this group and the polyphyly of individuals classified as *C. umbellata*. At the same time, genetic patterns emergent from two different genomic sampling methods exhibit notable differences that would not be apparent had only one method been applied. And graphics derived using each sequence sampling method exhibit notable differences according to two different analytical methods (phylogenetic tree versus split-tree networks). So there is not one result, but four different ones, even as these agree on several points. Moreover, about 10% of sampled individuals could not be classified into a lineage, and the number of unclassifiable individuals was the same as the number of lineages classified. This result will be reconsidered below.

Another illustrative example is the phylogenomic analysis of columnar cacti (Cactaceae; Pachycereeae) by Copetti et al. (2017). The data demonstrated rampant gene tree conflict, which the authors attributed to incomplete lineage sorting dating back to Cactaceae origins. This, in turn, was explained as a consequence of especially long generation times combined with moderate effective population sizes (but see Gorelick 2009). Again, the phylogenomic investigation yielded useful and potentially paradigm-shifting discoveries. The results may offer insights into the (pleisiomorphic) capacity for intergeneric hybridization among some cacti, as well as graft compatibility. The results recall the notion that, indeed, cacti are a hypervariable "big genus" of classical Portulacaceae. But, notwithstanding the massive data, the analysis did not resolve cladistic phylogeny as conventionally conceived.

The phylogenomic data suggests reconceptualization of existing "species concepts." The results of Stoughton et al. (2017a) are consistent with the dynamic "wave model" of species that I developed in a privately circulated manuscript. That work advocated a distinction between "apospecies" and "synspecies," perhaps better termed "synapospecies," though not in the cladistic sense. Synspecies correspond to operational species, or groups of individuals classified as taxa or lineages. Apospecies are individuals that cannot be so classified. "Type specimens" perfunctory to formal taxon recognition, are, by definition, apospecies, because their diagnosis tautologically asserts that they are different from other species, without otherwise ascribing to them species qualities other than as Platonic ideals. But the taxonomic recognition/acceptance of the hypothetical species does not depend per se upon their status as apospecific (unique). After all, no two individuals are exactly alike. Rather, operational specific status depends on the existence of a real or hypothetical class or category of individuals conspecific to the Type individual and apospecific to the Type of any other species. This class comprises the hypothetical synspecies.

To appreciate the preceding, imagine that the ancestors of the individuals classified into eight taxa in Stoughton et al. (2017a) had never proliferated or, alternatively, were surviving individuals of lineages that had proliferated but died out. And imagine that the history/fate of the eight individuals not classified into taxa likewise was reversed, i.e., that each of them had proliferated. No biological or evolutionary law constrains these possibilities. The pattern of taxa evident in Stoughton et al.'s (2017a) figures would be "inverted." The singletons would be the taxa and the taxa would be the singletons

Alternatively, suppose that *no* individuals currently existed *except* the eight Type specimens of the recognized taxa and the eight unclassified individuals. The figures would illustrate parametric relations between 16 apospecific individuals, i.e., 16 individuals not conspecific with any other. Possibly all 16 individuals would be classified as one to up to 16 operational species, depending on taxonomic inclination. In any case, the nonindependence and nonidentical distribution of species should be clear. Operationally, the eight lineages recognized by Stoughton et al. (2017a) are thus synspecies, and their Types and the unclassified individuals apospecies.

The results of both Stoughton et al. (2017a) and Copetti et al. (2017) also suggest reconceptualization of the relation between "gene trees" and "species trees." Although it has been recognized for decades that the former are distinct from the latter (e.g., Doyle 1992), this conceptualization is nuanced. It emerged from the deduction that an individual gene tree might be in conflict with or otherwise misrepresent a species tree. This trivial conceptualization has persisted into the phylogenomics era, in which the species tree evidently is equated with that of a plurality of concordant loci trees (e.g., Copetti et al. 2017). In other words, the "true" species tree is defined mathematically as the phylogenomic consensus.

But the conceptualization of species as gene tree consensus is flawed epistemologically. In particular, the Type of a species ontologically refers to the entirety of its tangible characteristics, including its DNA sequences. The gene trees are irrelevant. If the phylogenetically "minority" genes were excised, even a single lineage-sorted allele, the individual would be different ontologically. This should be self-evident in the case of hybrid species, whose ontological identity precisely specifies their possession of genes of different lineages.

The paradox is resolved if it is appreciated that gene and species trees are *ontologically* distinct: they *neither* agree *nor* conflict with each other. This can be appreciated in the context of hierarchy theory (e.g., Salthe & Matsuno 1995; Yarrow & Salthe 2008; Fábregas-Tejeda &Vergara-Silva 2017). In particular, genes and species are dynamical self-organizing systems separated hierarchically by several levels. But evolution at each hierarchical level is influenced mainly by proximal, less so distal, levels. Systems thus evolve as constrained by a subordinate level, which establishes starting conditions, and a superimposed one, which establishes a (transitory) boundary. The consequence is that, via percolation, different hierarchical levels evolve coordinately but not in lock step.

Per hierarchy theory, a "species tree" is the continuous evolutionary history of the ontogenetic phenotypes (Maturana & Mpodozis 2000) of its individual members. A gene tree is the continuous evolutionary history of a DNA locus. DNA replication provides the initial conditions for sequence evolution; the genome is the upper boundary. DNA sequences provide the initial conditions for genome evolution; a cell is the upper boundary. And so forth, up to the level of species and the environment. Note that each level is free to "improvise" as long as the improvisation is tolerated at adjacent levels (i.e., maintains structural coupling). But failure at any level imposes failure at all levels, even though other levels are functioning "normally." Evolution at different levels is semi-coupled. Levels function interdependently, yet independently, A change at one level does not "cause" change at another level except in the trivial case that the change is lethal. Thus, gene and species

histories differ not because they differ empirically, but because they differ ontologically and do not directly *impose* common histories on each other.

4. Montiaceae Phenotypic, Cytological, and Ecological Evolution

4a. Habitat/niche diversity. Montiaceae species distinguish from other Portulacineae phylogeographically, ecologically, and phenotypically. Their distribution concentrates in the high-relief and climatically diverse temperate zone westwards from the American high cordillera (cis-cordilleran), with lesser additional native diversity east of the American cordillera (trans-cordilleran). The cis-cordilleran diversity extends circum-Pacifically to Siberia, Australia, New Zealand, and the Kerguelen Islands (Hershkovitz 2018a, b). Other Portulacineae are distributed mainly more towards the tropics and from the American high cordillera eastwards (trans-cordilleran) and extending to Africa/Madagascar, with a few taxa in warmer parts of Australasia/Oceania (Hershkovitz 1993a, 2018c; Ogburn & Edwards 2015). While early-diverging Montiaceae share with other Portulacineae a more warm/arid distribution and succulence, later-evolved lineages concentrate especially in cooler/moister (higher altitude and/or latitude) environments and are less or not succulent (Ogburn & Edwards 2015; Hershkovitz 2018c).

Montiaceae niches are diverse. Their habitats range from desert to aquatic and arctic/alpine to subtropical. Considerable habitat diversity characterizes not only the family as a whole, but several of the included genera. Habitats within the genus *Phemeranthus* alone range from conditions as hot or hotter than those of any other Portulacineae, to cool temperate montane, and even bogs (Price 2012; Ocampo 2017). Calyptridinae comprises ca. 23 mostly arid-adapted taxa in four genera: (1) the arid-region high alpine monotypic genus *Lenzia*; (2) *Philippiamra*, which includes arid alpine and hyperarid desert species that possibly are the most drought-resistant of all vascular plants (Hershkovitz 2018c; cf. Bahamondes et al. 2012: *15*; see also below); (3) *Calyptridium*, which includes ca. 11 taxa whose habitats range from sea-level to alpine, and from the Sonoran and Mojave Deserts to southern Oregon mountains receiving ca. 500 mm mean annual precipitation (MAP); and the peculiar monotypic desert taxon *Thingia*. Perhaps a more extreme example is *Claytonia* sect. *Claytonia*, whose 28 taxa distribute disproportionately in cool, moist habitats. Yet, the habitats of the genus range from the Mojave Desert (ca. 5 mm MAP) to Vancouver Island (ca. 5000 mm MAP), and from Arctic vegetation limits to the warm temperate S/SE US and Mexico. In all of these genera, the extremes span relatively low genetic divergences indicative of Pliocene or more recent diversification.

Montiaceae include species that span small to large ranges and rare to common frequencies. As discussed in Hershkovitz (2018b, c; see also below), seven species of Montiaceae have become adventive intercontinentally to varying degrees. These include one species of *Phemeranthus*, one of *Calandrinia*, two of *Claytonia*, and three of *Montia*. An additional species of *Montia* considered adventive by O'Quinn et al. (2005) likely is not (see below). The Chilean *Cistanthe laxiflora* (Phil.) Peralta & D.I. Ford possibly has become adventive in California.

As will be elaborated better in revisions of Hershkovitz (2018b, c), there seems to be no evolutionary or ecological rhyme or reason to explain, much less predict, adventive establishment among Montiaceae or, for that matter, probably among biological organisms in general. Hypotheses and conclusions advanced to explain species "invasiveness" base on statistical fallacies such as those described in Hershkovitz (2018c).

Montiaceae diversification has been thought to be related to the diversity of the local habitats in the main range of the family, far-western North America and South America (Hershkovitz 2006; Ogburn & Edwards 2015). But Hershkovitz (2018c) reconsidered this view, pointing out that some Montiaceae lineages in this range never diversified (e.g., the monotypic genera *Lenzia* and

Lewisiopsis), while *Rumicastrum*, the largest genus in the family, is endemic to less macroecologically diverse/extreme regions of Australia (see below). The same phenomenon characterizes many lineages of angiosperms in macroecologically diverse western America: some have diversified and some have not. Similarly, other angiosperm lineages have diversified exceptionally in relatively macroecologically less diverse regions of South Africa and Australia. Thus, local macroecological diversity is neither necessary, nor sufficient, to explain Montiaceae diversity. The criterion of necessity and sufficiency of evolutionary explanation was emphasized in Hershkovitz (2018c) and emerges again below.

4b. Growth form and life history diversity. Montiaceae also differ from other Portulacineae in comprising mostly hemicryptophytic (including acaulescent rosettiform-caudiciform) perennials and therophytes (Hershkovitz 1993a, 2018c; Ogburn & Edwards 2015). Other Portulacineae comprise mostly phanerophytic to chamaephytic herbs, shrubs, trees, and vines, and often stem succulents. However, annuals occur among *Portulaca* (Portulacaceae) species (Ocampo 2012), and most Anacampserotaceae species are hemicryptophytes, a few acaulescent (Carolin 1987, 1993; Rowley 1994). Phylogeny of extant Montiaceae implicates at least 14 life history transitions since the split between Cistantheae and Montioideae, 25–35 million years ago, out of the total ca 16 transitions among all Portulacineae over 50+ million years (Ogburn & Edwards 2015; Hershkovitz 2018c; age estimates of Yao et al. 2019 are rather older, discussed further below).

4c. Relation of life history evolution to temperature niche. Ogburn & Edwards (2015) reported a statistically significant higher rate of phylogenetic temperature niche diversification among Montiaceae compared to other Portulacineae. They also reported a phylogenetic correlation between life history and temperature niche, resulting in annual/perennial distributional sorting into, respectively, warmer/cooler habitats. They attributed the distribution bias to the shorter growth season of cooler environments, which they supposed is insufficient for annuals to complete their life cycles. They concluded that the Montiaceae ancestor was an acaulescent rosettiform tap-rooted perennial species that, during phylogenesis, repeatedly gave rise to annual species in response to temperature-mediated. This selection, in turn, was enhanced by the heterogeneity of temperature niches across short geographic distances in mountainous western America. Ogburn & Edwards (2015) also concluded that the evolutionary lability of life history among Montiaceae, which facilitated their temperature niche diversification, was a function of their acaulescent rosettiform growth form. This, they supposed, facilitated evolutionary lability of above-/ below-ground biomass allocation.

Hershkovitz (2018c) rejected Ogburn & Edwards' (2015) interpretations, arguing that these owed to a combination of data, statistical, computational, and epistemological artifacts. Among these:

1. Hershkovitz (2018c) concluded that, while the Montiaceae ancestor likely was perennial, contrary to earlier interpretations, including Hershkovitz (1993a), most perennial Montiaceae species/clades were derived from annuals. Goolsby et al.'s (2018a, b) results for *Calandrinia*, if correct, further support this conclusion.

2. Ogburn & Edwards (2015) lumped perennial life forms that are not homologous, i.e., caudiciform, rhizomatous, and pachycaul forms. This evidently biased their statistical analysis (see also below).

3. Ogburn & Edwards (2015) used global climate temperature data as a proxy for plant temperature niche. Hershkovitz (2018c) pointed out that climate temperature values can depart substantially from plant microenvironment temperature values (Körner & Hiltbrunner 2018).

4. Ogburn & Edwards (2015), used species "mean" climate temperature values in their analysis, these calculated based on database collection localities. The view here is that species are not statistical units (see above), but, even so, their extreme values are more relevant than their means, since they approximate better the realizable niche range. Many factors determine plant incidence, e.g., competition, so that mean observed values might not and probably do not reflect physiological optima. Moreover, the method is subject to multiple sources of error: collection bias, databasing bias, misidentification, and taxonomic classification artifact.

5. Ogburn & Edwards (2015) conclusions fail the test of causal necessity and sufficiency. In multiple instances, annuals occur in cold environments and perennials in warmer ones. Five annual species in three genera (*Calyptridium*, *Montiopsis*, and *Philippiamra*) are strictly (sub-) alpine. Two more are facultatively so. Numerous perennial species of several genera (*Cistanthe*, *Claytonia*, *Lewisia*, *Phemeranthus*, and *Rumicastrum*) are distributed in warm environments, occurring alongside annual Montiaceae species. There are both annual and perennial species having very broad temperature niches.

6. As alluded to above, ecological heterogeneity is neither necessary nor sufficient to promote diversification. Some taxa, e.g., *Lewisiopsis*, failed to diversify under the same geographic/ ecological conditions as co-occurring Montiaceae. As noted, *Rumicastrum* is the most diversified genus in the family, yet distributes across Australia, which is ecologically more homogeneous than western North America or South America.

7. Hershkovitz (2018c) disputed the notion that growth season length restricts annuals to warmer environments, noting that the growing season of the warmer desert habitats of Montiaceae is much shorter than the cold alpine ones. Interestingly, the annual life history evidently is an adaptation to *short* growing season in the C4 species *Portulaca oleracea* L. (Portulacaceae). Among *Portulaca* species, range of the latter extends by far furthest into the cool temperate zone. Here, light/temperature are insufficient to accommodate the physiological requisites of perennial C4 species. But their seeds may be perfectly cold-hardy, so an annual life history is possible.

8. Ogburn & Edwards (2015) presented no evidence supporting their assertion that life history evolution among Montiaceae reflected optimization of above-/below-ground biomass allocation. Hershkovitz (2018c) disputed this notion and presented a more plausible and empirically-evidenced argument that the life history transitions originated consequent to temperature sensitivity of reproductive induction, later differentially fixed by genetic assimilation in different temperature environments.

4d. Moisture niche evolution among Montiaceae. The overall phylogenetic trend among Montiaceae has been towards cooler/moister niches. The earliest diverging lineages (Phemerantheae, Cistantheae, and *Rumicastrum*) comprise often warmer and mainly arid- to hyperarid-adapted taxa. Most of these taxa are succulent or, in the case of *Montiopsis* species, (glandular-)pubescent. Nonetheless, some species of these genera evolved into cooler/moister niches, e.g., a subaquatic *Phemeranthus* species (Ocampo 2017), more southerly Chilean (ca. 38S) and northern Chilean coastal fog desert species of *Cistanthe*, more southerly Chilean (ca. 40S) populations of *Montiopsis,* and southern Oregon populations of species of the otherwise xerophytic genus *Calyptridium.* The successively diverging lineages, *Calandrinia*, Hectorelleae, and Montieae, trend to moister niches.

But some species of Montiinae, in particular *Claytonia* sect. *Claytonia*, also have evolved back into more arid niches of the south central and SW US and Mexico (O'Quinn et al. 2005; Stoughton et al. 2017a, b). These taxa thus converge on the geographic range shared by *Phemeranthus* and other arid-adapted Portulacineae, e.g., species of Anacampserotaceae, Cactaceae, Portulacaceae, and Talinaceae.

Below is a description of precipitation/moisture niche extremes that occur among Montiaceae genera and major subgeneric taxa, all approximated from distributional data and general climate maps.

1. *Phemeranthus*: Sonoran Desert (< 100 mm MAP) to SE US (ca. 1500 mm), with one subaquatic species in Mexico (Ocampo 2017).

2. *Cistanthe* sect *Cistanthe*: Hyperarid Atacama Desert (< 50 mm) to seasonally moist south central Chile (500–1500 mm).

3. *Cistanthe* sect *Rosulatae*: Hyperarid Atacama Desert (< 50 mm) to moderately wet south-central Chilean Andes (ca. 2000 mm).

4. *Calyptridium*: Mojave and Sonoran Deserts (< 50 mm) to the Klamath Mountains, southern Oregon (ca. 1500 mm).

5. *Thingia*: Mojave and Sonoran Deserts (< 50 mm).

6. *Philippiamra*: Atacama Desert vegetation limit ("zero" to < 50 mm) to arid alpine Andes (ca. 500 mm).

7. *Lenzia*: Arid alpine (ca. 300 mm).

8. *Montiopsis* subg. *Montiopsis*: Atacama Desert (< 50 mm) to moderately wet south-central Chilean Andes (ca. 2000 mm).

9. *Montiopsis* subg. *Dianthoideae*: Seasonally dry to moderately wet south-central Chilean Andes (ca. 600–2000 mm).

10. *Rumicastrum*: Arid western Australia (< 50 mm) to moderately wet NE Australia (ca. 2000 mm). Data from Hancock et al. (2018) indicate that arid/wet transitions occurred multiple times.

11. *Calandrinia*: Desert/semi-desert (ca. 100 mm) to more or less persistently wet S Chile and Pacific NW N America (> 5000 mm). Some perennial species are subaquatic, restricted to bogs and streams.

12. Hectorelleae: Persistently wet habitats (1000 to > 5000 mm; see Wagstaff & Hennion 2007).

13. *Lewisiopsis*: Seasonally dry (ca. 1500 mm).

14. *Lewisia* sect. *Lewisia*: Seasonally moist sites of the Sonoran and Mojave Deserts (ca. 200 mm) to persistently wet Pacific NW N America (ca. 5000 mm). Some species occur in bogs or boggy sites (Davidson 2000).

15. *Lewisia* sect. *Cotyledon*: Central Sierra Nevada Mountains (ca. 1500 mm) to persistently wet Pacific NW N America (ca. 5000 mm).

16. *Montia*: Seasonally arid (ca. 1000 mm) to persistently wet (ca. 5000 mm). One species is subaquatic to aquatic.

17. *Claytonia* sect. *Claytonia*: Seasonally moist SW US deserts (ca. 200 mm) to persistently wet Pacific NW N America (ca. 5000 mm). Data of Stoughton et al. (2017a) indicate that the arid/wet transition occurred twice.

18. *Claytonia* sect. *Limnia*: Seasonally moist SW US deserts (ca. 200 mm) to persistently wet Pacific NW N America (ca. 5000 mm).

19. *Claytonia* sect. *Rhizomatosae*: Seasonally moist Mediterranean and Great Basin areas (ca. 1500 mm) to persistently wet Pacific NW N America (ca. 5000 mm). Some species occur in bogs.

I add the observation that MAP is a misleading indicator of moisture availability (see also below). In Montiaceae country in southern California and more so in northern Chile, the precipitation regime is bimodal. MAP averages rainfall of cyclically very wet and dry years, so that the "average" is not modal. In the high relief American range of Montiaceae, much to most plant irrigation is via runoff rather than localized precipitation. And many Montiaceae denizens in Chile/Peru are irrigated mainly by fog. In any case, among Montiaceae, at least 10-fold arid/wet precipitation transitions have occurred at least (and probably more than) 10 times in a clade of ca. 300 modern taxa. Subaquatic/aquatic species have evolved at least five times. The low genetic divergence within clades suggest that most of these transitions occurred relatively rapidly, perhaps over the course of < 5 million years.

Ogburn & Edwards (2015) found no evidence of increased phylogenetic diversification of Montiaceae precipitation niche relative to other Portulacineae and no correlation between precipitation niche and life history diversification. Presumably, precipitation niche was considered to be a proxy for moisture niche. Hershkovitz (2018c) argued that Montiaceae, contrary to Ogburn and Edwards' (2015) conclusions, indeed have experienced a greater rate and degree of moisture niche diversification relative to other Portulacineae.

Although I do not provide a detailed accounting here, moisture niche evolution among remaining Portulacineae has been less and slower. Although the largest family, Cactaceae (1500–1900 spp.), spans considerable precipitation niche breadth, the species are restricted overwhelmingly to arid habitats. On a cladogenetic basis, cactus moisture niche evolution has been infrequent and slow. Moisture niche is narrow among Anacampserotaceae and Didiereaceae, broader among Basellaceae and Talinaceae, broadest among Portulacaceae. In the latter three families, perhaps significantly, the species occurring in the wet end of the precipitation spectrum (>3000 mm) are weedy/invasive and/or escapes from cultivation. Thus, while many, probably most, other Portulacineae species evidently are obligate xerophytes, unlike Montiaceae, other Portulacineae include no obligately hydrophytic or subaquatic species. In contrast, while many Montiaceae species are as xerophytic as any other Portulacineae and they include arguably the *most* xerophytic vascular plant species (viz., *Philippiamra* spp.), the family also includes also several hydrophytes.

Hershkovitz (2018b) explained Ogburn and Edwards' (2015) results partially as a consequence of their using precipitation as a proxy for moisture niche. The discrepancy between precipitation climate data and physiological moisture niche is even greater than that for temperature niche. Hershkovitz (2018b) described a well-known summer alpine botanizing locality at a ski resort near Santiago that harbors at least 11 Montiaceae species in 4 genera. The species share the same precipitation niche but occupy microenvironmental moisture niches ranging from physiologically xerophytic (*Cistanthe* spp.) to more or less mesic (*Calandrinia* and *Montiopsis* spp.) to boggy (*Calandrinia* spp.) to aquatic (*Montia fontana* L.). Hershkovitz (2019b) noted that the large succulent *Cistanthe subspeciosa* Hershk. thrives in hyperarid Atacama desert flats because of mountain runoff. Also, precipitation obviously ignores evapotranspiration potential, which is a function of humidity and temperature. For example, some Chilean/Peruvian Montiaceae are restricted to desert fog oases, where fog precipitation is not recorded, or, if recorded, amounts to perhaps 10–20% of the equivalent rainfall necessary to support the incident physiognomy. Thus, using precipitation data as a proxy for moisture niche severely distorts the estimated rate and degree of evolution of the latter.

In addition, Ogburn and Edwards (2015) analyzed only resolved cladistic nodes, whereas extreme differences in moisture niche occur within genera whose interspecific relations are poorly resolved (see above). The poor resolution, in turn, is consequent to rapid evolution. They also recorded precipitation niche as a function of the mean of few collecting localities, thus ignoring the extremes of widespread species, which also reflect rapid evolution. Thus, and quite remarkably, Ogburn and Edwards (2015) not only effectively ignored much, if not most evidence of Montiaceae moisture niche diversification, they also overlooked the short evolutionary time with which this diversification had occurred.

4e. Succulence and other xerophytic adaptations among Montiaceae. Especially among the earlier-diverging lineages, Montiaceae include many leaf-succulent species. Ogburn and Edwards (2015) hypothesized that succulence should be phylogenetically correlated with low and/or seasonally distributed precipitation, finding only the former relation. As above, presumably they believed that precipitation proxied for moisture niche. Ogburn and Edwards (2010) earlier had noted that not all arid-adapted plants are succulent and not all succulent plants are arid-adapted. Hershkovitz (2018c) pointed out that indeed Montiaceae include several non-succulent but otherwise arid-adapted species (*Montiopsis* spp. and *Lenzia*) and degrees of succulence occur in bog species. Thus, (possibly even mesophytic) succulent ancestors can evolve nonsucculent xerophytic descendents. The analysis of Ogburn and Edwards (2015) lumped arid-adapted with non-arid-adapted taxa and also lumped xeric and moist microhabitats within the same precipitation zone. The premise of the hypothesis that succulence should correlate phylogenetically with precipitation thus is unexplained.

4f. Polyploidy and Montiaceae diversification and ecological evolution. This section reconciles evidence for a hypothetical relationship between whole genome duplication (WGD) and phylogenetic/ecological diversification of Montiaceae. Considerable theoretical attention over the past two decades has focused on the historical contribution of WGD, in particular autopolyploidy, to plant phylogenetic and ecological diversification (D. Soltis et al. 2014, 2016; P. Soltis et al. 2015; see also Gorelick & Olson 2011; Levin 2019). One premise, among others, is that duplicating all loci facilitates locus subfunctionalization, hence both taxonomic and ecological diversification.

Polyploidy consequent to cytokinetic failure is the prevalent mechanism of WGD. In theory, a genome could duplicate entirely via short infra-chromosomal tandem repeats, or by successive partial chromosome duplications. In a different parametric dimension, polyploidy is an extreme form of DNA sequence duplication, the minimal form being a single DNA base duplication. But the latter is a duplication within the DNA-level hierarchy, which the chromosomal level absorbs. Polyploidy and all other forms of heteroploidy occur within the chromosomal hierarchical level and subsume the DNA level along with it.

Allopolyploids, consequent to hybridization, share with autopolyploids the feature of duplicated loci and might be expected to manifest the same evolutionary consequences (Hegarty & Hiscock 2008). However, it is difficult to dissect the consequences of polyploidy from those of hybridization per se, as the latter immediately creates a distinctive phenotype, with additional diversity segregating in progeny. More problematic, the distinction between allo- and autopolyploidy can be blurred on both subjective and objective bases. Allopolyploidy presumes hybridization between taxonomically distinct parents, but this distinction is subjective.

While allopolyploids can be diagnosed on positive evidence (allozymes, genomic evidence), the absence of such evidence does not rule out allopolyploidy. The diploid progenitors of a highly divergent allopolyploid might be extinct or otherwise genomically highly modified. Moreover, the effects of allopolyploidy might occur in hybrids between differentiated genotypes within the same taxon, even genomically very similar ones. A single allele in one of two otherwise genomically identical parents might cause polyploidy in the offspring. This “cryptic allopolyploidy” creates

"pseudo-autopolyploidy." The consequence is that in phylogenetic time and space, autopolyploidy will tend to be overestimated.

Chromosomal data exist for less than half of Montiaceae species, and most reports represent single or very few sampled individuals. Moreover, the reports are scattered in the literature, some of them in obscure and/or unpublished theses. There exists nothing close to a monographic accounting, a task beyond the scope of the present work. By far, the genus most thoroughly studied cytologically is *Claytonia* (Miller & Chambers 2006), and this genus and its taxonomic species are notoriously heteroploid. Complete species sampling is available for *Montia* (Heenan 2007; Miller & Chambers 2012a) and *Montiopsis* (Ford 1992), with considerable species data available for *Calyptridium* (Guilliams & Miller 2014), *Lewisia* (Mathew 1989; Hershkovitz & Hogan 2002, 2003), and *Phemeranthus* (Price 2012). Few counts are available for *Calandrinia*, *Cistanthe*, and *Rumicastrum* (e.g., Wickramasinghe et al. 2009; Marinho et al. 2019), and apparently none for *Philippiamra*, *Thingia*, *Lenzia*, or *Lyallia*. Polyploidy is reported in *Claytonia*, *Lewisia*, *Montia*, *Montiopsis*, and *Phemeranthus*, and it is the base condition in three genera (*Calyptridium* and the monotypic genera *Hectorella* and *Lewisiopsis*; Hinton 1975; Mathew 1989; Wagstaff & Hennion 2007; Heenan 2007). Aneuploidy/dysploidy are common in all examined polytypic Montieae, i.e., *Claytonia*, *Lewisia*, and *Montia*, and is evident in *Rumicastrum* (Wickramasinghe et al. 2009).

Only two studies have analyzed the evolutionary consequences of polyploidy among Montiaceae in a hypothetico-deductive framework. One is McIntyre (2012), who studied the relation of polyploidy and habitat in 2–6x *Claytonia perfoliata* Donn ex Willd. complex populations. The other is Smith et al. (2017; see also Yang et al. 2018), who attempted to align phylogenetic WGD events with habitat shifts among all Caryophyllales, including some Montiaceae. Both studies were similar to Ogburn and Edwards (2015) in using climate temperature and precipitation data as surrogates for ecological niche. Thus, the same criticism as above applies, as does the epistemological criticism of confounding correlation with cause (Hershkovitz 2018c).

Notably, in this case, different investigations of the same phenomena (phylogenetic and ecological diversification) consider the hypothetically plausible consequences of evolution of one parameter (polyploidy or life history) while mutually ignoring the hypothetically plausible consequences of the other. Hershkovitz (2018c) pointed out this statistical fallacy, which is epidemic in the contemporary evolutionary biology paradigm generally (see below).

McIntyre (2012) noted that both autopolyploidy and allopolyploidy occur in the *Claytonia perfoliata* complex, but he did not specify the condition of the study populations. Smith et al. (2017) likewise did not distinguish between allopolyploidy and autopolyploidy. Thus, neither study validly evaluated the effect of ploidy per se. But these points are moot, since neither study yielded evidence sufficiently convincing to attribute phylogenetic or ecological diversification to polyploidy.

Hershkovitz (2018c) disputed the significance afforded autopolyploidy in explaining phylogenetic/ecological diversification, as revision of that work will elaborate. Lack of autopolyploid necessity and sufficiency was emphasized. Two monotypic polyploid Montiaceae taxa, *Hectorella* and *Lewisiopsis*, evidently are octaploids that have diversified much less than their close relatives. Moreover, *Lewisiopsis* shares the same geography, ecology, and growth form that are supposed to explain Montiaceae diversification in general. Hershkovitz (2018c) suggested that, in this case, polyploidy may have sequestered its diversification (see below). There is no shortage of other examples among plants contradicting the supposed relation between polyploidy and diversification, nor, for that matter, the supposed relation between any two variables in the course of evolution.

Other evidence inconsonant with the supposed polyploidy/diversification relation is more sublime.

1. Soltis et al. (2007) noted that accepted taxonomic species commonly include both diploid and autopolyploids. Possibly or potentially they can be distinguished phenotypically but evidently not sufficiently to be distinguished taxonomically by excellent taxonomists. Heteroploidy especially of *Claytonia* spp. demonstrates this (Miller & Chambers 2006).

2. Kubešová et al. (2010) reported an *inverse* correlation between genome size and plant species invasiveness (effectively, ecological adaptability). They attributed this to the metabolic cost of DNA/chromosome replication, hence greater reproductive efficiency of genomes with little "junk" DNA. Although polyploidy per se was not addressed directly, one can infer from Kubešová et al.'s data (2010) that polyploidy possibly has a neutral or negative effect on invasiveness. In particular, 20/47 (43%) species they characterized as merely "naturalized" in the Czech Republic are diploid. But a *higher* proportion (20/40; 50%) of diploids were "invasives."

3. Polyploidy has additional evolutionary disadvantages (see, e.g., Gorelick and Olson 2011). Meanwhile, Smith et al. (2017), Yang et al. (2018), and other WGD researchers, advertise only hypothetical WGD advantages and do not consider, much less model and supercompute, its costs.

4. In an analysis of *Castilleja* (Orobanchaceae), Tank and Olmstead (2008) concluded that the deleterious effects of polyploidy promotes the evolution of longer generation times, which, in turn, decreases the rate of phylogenetic and ecological diversification. But Smith et al. (2017) seem to maintain that polyploidy is associated with faster ecological diversification. This seems to be a contradiction.

As an epistemological criticism, Hershkovitz (2018c) emphasized that polyploidization and organismal diversification are concurrent and sequential biogenetic processes operating at well-separated organizational levels. Superimposing the history of one over the other is bound to yield some degree of temporal coincidence, as Smith et al. (2017; Yang et al. 2018) conceded. Arguments for a cause /effect relationship are specious, if not frivolous. This is so especially given the lack of necessity/sufficiency evidence at the infraspecific level, and the axiomatically increasing ambiguity of historical evolutionary/ecological reconstruction at deeper phylogenetic levels. Indeed, organismal diversification might involve subfunctionalized loci duplicated consequent to polyploidization. But this may be exaptation rather than adaptation, and it is not bound to occur. In short, the evolutionary consequence of polyploidy seems to be no more or less than polyploidy itself.

4g. Montiaceae leaf morphological/anatomical evolution. One would suppose that the morphology and anatomy of photosynthetic organs figure prominently in ecological adaptation and evolution. As noted, most Montiaceae are rosette-forming annuals and perennials. Their leaves, accordingly, appear superficially similar, even monotonous (Hershkovitz 1991f, 1992, 1993b). The leaf shape most commonly is oblanceolate to spathulate but ranges from linear to broadly obovate. Sometimes the blades are essentially sessile, but often the blade is tapered basally into a broad petiolar region. In some species, especially among annual *Claytonia*, the petiolar region may be 5–10 cm or longer. Regardless, the leaf base among Montiaceae usually is broad to clasping, in a few species amplexicaul to perfoliate.

The exception to this generalized form is in Phemerantheae and possibly several but not all *Rumicastrum* species (which I have not studied in detail). Phemerantheae species have linear, succulent leaves and an extremely short but more distinct petiole. The basal portion of the blade is flanged and clasps the stem. Some *Rumicastrum* species have succulent, linear leaves that resemble Phemerantheae leaves, but other species have leaves more typical of other Montiaceae.

Commonly, leaves of perennial species are basal or suprabasal on unelongated internodes. However, in suffruticose and pachycaul *Cistanthe* species, the stems are leafy. Meanwhile, leaves of

annual species of annual/perennial genera commonly are both basal and distributed along the flowering stems, as in annual species of *Cistanthe*, *Calyptridium*, *Rumicastrum*, and *Calandrinia*. In these taxa, the stem leaves are morphologically/anatomically similar to the basal leaves. However, flowering stems of *Claytonia* species have only a single pair of sessile foliaceous bracts. In some species, these bracts resemble the basal leaf blades in size and anatomy. In some *Philippiamra* species, the flowering stem leaves are bract-like and succulent. Nonetheless, they appear to be the principal photosynthetic organs, remaining green long after the basal leaves have senesced. At that point, the shoot system may break from the root and form a sort of tumbleweed. All species of *Montia* have leafy stems, but in the rhizomatous species *M. parvifolia*, these are arranged in rosettes resembling those of caudiciform Montiaceae.

Leaves are entire except for some species of *Lewisia* sect. *Cotyledon* (Hershkovitz 1992). The petiolar region in some species of *Montiopsis* also may be dentate (Hershkovitz 1993b). Leaf serrations may be vascularized or not in *Lewisia*, but apparently are not in *Montiopsis*. In both of these genera, species with both dentate and entire leaves often have dentate sepals.

Given the similarity in gross leaf morphology, Montiaceae leaf anatomy, especially venation pattern, is surprisingly diverse (Hershkovitz 1991f, 1992, 1993b). This diversity proved to have taxonomic significance and was critical to the development of the current taxonomy of Montiaceae and Portulacineae generally. In fact, I had interpreted my preliminary Portulacineae leaf morphological/anatomical data in the classical Aristotelian taxonomic framework and according to prevalent notions of orthogenetic trends (Hershkovitz 1986). I realized my error literally days later, and this is what prompted me to change my dissertation focus from Nyctaginaceae to Portulacineae.

Several Montiaceae taxa can be diagnosed on the basis of leaf characteristics alone. For example, leaves of almost all *Calandrinia* species have a distinctive intramarginal vein and also distinctive epidermal morphology (see below). Montiinae leaves also have an intramarginal vein, but its configuration at the leaf apex is very different from *Calandrinia*, and the epidermal characters also are different. Venation and stomata of *Lewisia* are highly variable but very different from its sister, Montiinae. Leaves of *Calyptridium*, *Cistanthe,* and *Philippiamra* have weakly organized brochidodromous venation and brachyparacytic stomata.

Finer leaf veins in many taxa are distinctively sinuous and laminar or "ribbon-like," a single cell layer thick and up to at least 11 xylem elements broad. Annular protoxylem elements situate on one side, intergrading to scalariform-reticulate metaxylem elements on the other. These laminar veins are characteristic also of Phemerantheae, Cistantheae except *Lenzia*, and many *Rumicastrum* species. Among other Portulacineae, they are evident in certain Anacampserotaceae and Talinaceae. Apparently they occur in no other vascular plants.

Three-dimensional (3D) venation characterizes Phemerantheae, many if not most *Rumicastrum* spp., *Thingia*, and one species of *Lewisia,* and at least some portion of veins in the most succulent *Cistanthe* spp. (Hershkovitz 1991f, 1992; Ogburn & Edwards 2013). 3D venation also occurs in Anacampserotaceae and Portulacaceae (Hershkovitz 1991f, Ogburn & Edwards 2013). Hershkovitz (1991f, 1992, 1993b) also reported preliminary data on other venation characteristics, such as branching anatomy of finest veins and veinlet number per smallest vein enclosure.

Current phylogenetic evidence permits only a few insights on the evolution of Montiaceae venation characteristics. For example, the distribution of laminar veins in other Portulacineae and within Montiaceae, suggests that these may represent an ancestral condition in the family. These appear to have been lost in *Lenzia* and *Montiopsis* (Cistantheae), whose leaves are small and have poorly and irregularly structured venation. In fact, the evidence suggests that in the evolution of these genera, leaves became highly reduced and cataphyll-like, as they remain in *Lenzia*. In *Montiopsis*,

non-succulent foliage leaves thus re-elaborated with a morphology/anatomy distinct from succulent Cistantheae. In conjunction, distinctive trichomes evolved in *Montiopsis*, and these possibly replace succulence as an adaptation to aridity. 3D venation may have evolved as a developmental by-product of extreme succulence, but apparently succulence is neither necessary nor sufficient to induce 3D venation. In particular, 3D venation characterizes nearly all species of *Portulaca*, including *P. oleracea*, whose leaves are broad, flat, and not especially succulent by Portulacineae standards. Presumably laminar veins function to accommodate leaf expansion/shrinkage in response to water potential fluctuations during development and at functional maturity. They were lost during the evolution of Montioideae and did not reappear in the more succulent/xerophytic taxa, e.g., *Lewisia.*

Leaf histological analyses of Montiaceae evidently are too few and far between to draw systematic and evolutionary conclusions. The data will not be reviewed here. Given the diversity in vasculature patterning and the interest in Montiaceae evolution from the standpoint of succulence and photosynthetic innovation, new systematic histological analysis should be fruitful.

Stomatal morphology distinguishes Montiaceae from other Portulacineae (Hershkovitz 1991f, 1992, 1993b). Montiaceae all have brachyparacytic or similar perigenous forms, in which 1–2(–3) pairs of lateral subsidiary cells divide and differentiate from epidermal cells adjacent to the guard cell mother cell. This form is characteristic of *Phemeranthus*, most Cistantheae, the few examined *Rumicastrum* spp., *Lewisiopsis*, a few *Lewisia* spp., and most Montiinae. Variations include tetracytic stomata in most *Calandrinia* spp. and laterocytic stomata restricted to several *Lewisia* species. Anomocytic stomata (lacking subsidiary cells) have been observed in a few *Calyptridium, Lewisia*, and *Montiopsis* species. All other Portulacineae have anisocytic or parallelocytic stomata with mesogenous devlopment, in which the subsidiary cells and guard cells all develop from the stomatal meristemoid. Hershkovitz (1991f) also reported preliminary data for stomatal index, size, and laminar distribution, but this has not been followed up with detailed analysis.

Most Montiaceae taxa have glabrous leaves: *Phemeranthus*, *Calyptridium*, *Thingia*, *Lenzia,* Montieae, and essentially all of *Cistanthe* and *Rumicastrum.* Known exceptions in the last two involve papillate epidermal cells in single species (Hershkovitz 1991f, 1993b, 2019b). Trichomes are characteristic of *Calandrinia* and *Montiopsis*, but they are structurally distinct in the two taxa. Most *Calandrinia* species have unicellular ribbed trichomes on the leaf and sepal margins (rarely on the laminar surface). *Montiopsis* leaves and sepals all have both glandular and nonglandular multicellular trichomes, and sometimes these are elaborated into echinate appendages. *Montiopsis* subg. *Montiopsis* species have, in addition, multiseriate simple and barbed hairs, these developed from intertwining of long single adjacent epidermal hair cells.

Hershkovitz (1991f, 1993b) briefly reviewed theoretical aspects of leaf development, form, and function, but could draw no conclusions regarding, e.g., why *Calandrinia* and Montiinae species should have an intramarginal vein and other Portulacineae not, or differences in stomatal subsidiary cell development and anatomy. I do not pretend to resolve these questions here. From an evolutionary perspective, two general findings of the leaf morphological research stand out:

1. *The contrast between the relative monotony of Montiaceae gross leaf morphology with the diversity of anatomical structure and, presumably, physiological functioning.* My 1980s preliminary investigations of leaf anatomy of Caryophyllales more broadly (including Polygonaceae and Plumbaginaceae) indicated that Montiaceae diversity was especially high. In other families, leaf venation and epidermal characteristics are relatively monotonous at the familial/subfamilial level.

2. *Evolutionary transitions from xerophytic to mesophytic leaf anatomy.* This occurred in conjunction with the origin of Montioideae. Xerophytic adaptations tend to be considered de

facto evolutionarily derived. They are at one level, but Montiaceae are an example of where mesophytic adaptations are derived. Succulence decreased and laminar venation was lost. Mucilagenous cells characteristic of Phemerantheae, *Cistanthe*, *Calyptridium*, *Thingia*, and *Philippiamra* also became reduced or lost in subsequently evolved taxa. Transition back to xerophytic leaves occurred in *Lewisia*, but the vasculature is distinct from that in the "paleomonts."

4**h. Montiaceae reproductive morphological evolution.** Reproductive morphological diversity among Montiaceae genera is described adequately by Carolin (1987, 1993) and Hershkovitz (1993a). There appear to be no particular phylogenetic trends at the familial level, so detailed descriptions will not be repeated here. In fact, the most notable aspect of reproductive morphology of Montiaceae is the degree to which historically it misled phylogenetic and taxonomic interpretation.

Many to most species of most Montiaceae genera have a generalized floral morphology that includes two sepals, usually 5(–9) petals, 5–∞ stamens, 3(–5) carpels, and numerous seeds. That the sepals are an involucre and the petals sepals (Dos Santos & De Craene 2016) is not important in this context. This general morphology characterizes *Phemeranthus*, *Cistanthe*, *Montiopsis*, *Rumicastrum*, *Calandrinia*, *Lewisiopsis*, *Lewisia*, and some *Philippiamra* species. Infrageneric variation in numbers of floral organs often is correlated positively with floral size, but not always, e.g., relatively small-flowered *Calandrinia* species have 6–8 petals and five carpels (Elvebakket al. 2015). Sepal number, however, does not vary except in one species of *Lewisia.* Meanwhile, Hectorelleae, *Calyptridium*, and certain species of *Philippiamra*, *Rumicastrum*, *Montiopsis*, and *Calandrinia* have small and reduced flowers with fewer than the standard number of petals, stamens, carpels, and/or seeds. Flowers in some *Calyptridium* and *Philippiamra* species occur in dense heads.

Fruits in most taxa are basipetally dehiscent valvate capsules, except *Lewisia*, in which dehiscence is acropetal. Indehiscent or irregularly dehiscent 1-seeded fruits occur in one or more species of *Calandrinia*, *Calyptridium*, *Philippiamra*, and *Rumicastrum*. Seeds in the family *mostly* are similar to those characteristic of all core Caryophyllales: lenticular to subglobose, 1–2 mm in diameter, embryo linear, curved, peripheral, and seed surface smooth to colliculate, black, and lustrous. Variation in all of these traits, as well as size, occurs at the generic and infrageneric level. *Cistanthe* is the most distinctive and variable genus. Most species have pustulate or hirsute seeds, and sculpturing can be tuberculate, granulate, or areolate. Tuberculate sculpturing occurs in species of *Calandrinia*, as well. The exotesta of most *Phemeranthus* species is pelliculate, and seeds of some species are sculptured with arctuate ridges (Price 2012). Several species of *Montiopsis* have brown seeds (Ford 1992). Strophioles occur in most *Cistanthe* and Montiinae species and in *Lewisiopsis*.

Ovule number among Montiaceae presumably is correlated with seed number, but not all ovules develop into seeds. Because most Montiaceae species descriptions at best report numerical seed counts (as opposed to, e.g., "numerous"), ovule numbers at best only can be estimated. An exception is among Montiinae: species of *Montia* and *Claytonia* sect. *Limnia* have three ovules, whereas remaining *Claytonia* taxa have six.

Arroyo et al. (2018, 2019) reported ovule counts in 178 incidental species of the central Chilean Andes, among these nine Montiaceae species. They tested in a Darwinian Modern Synthesis framework a hypothesis that, corrected for phylogeny, flowers of highest elevation species should have more ovules as a form of bet-hedging against pollinator scarcity/unreliability in extreme environments. The hypothesis found some statistically significant support, but in a method/ parameter-specific manner. I reject the conclusions on technical but mainly epistemological (see below) bases. Since the study is not Montiaceae-specific, I will not elaborate here a technical critique, except to note the axiom that if enough parameters are tested with enough methods,

statistical significance is bound to emerge somewhere. Similarly, in planar view, especially bright light from spatiotemporally remote stars may seem to form patterns.

In any case, the Montiaceae data did not seem to corroborate the hypothesis especially well. One higher elevation *Calandrinia* species had modestly more ovules than a lower elevation one, but a lower elevation *Montiopsis* species had about twice as many ovules as the higher elevation ones. Two incident alpine *Cistanthe* sect. *Rosulatae* species were not analyzed, presumably because both are higher alpine, and there is no lower alpine species in this zone for comparison. But my informal accounting indicates that these alpine species do not have higher ovule numbers than many lower elevation species of the section. Meanwhile, among *Cistanthe* as a whole, seed numbers per fruit and even more so per individual are highest in the numerous lowland *Cistanthe* sect. *Cistanthe* species (e.g., Hershkovitz 2018d).

Superficial examination of seed numbers in floristic descriptions of North American and Australasian Montiaceae species yields no clear pattern relation between ovule number and ecology. A further complication is that many Montiaceae species inhabit the desert, where pollinator scarcity/unreliability is at least as severe as it is in the high alpine. However, pollination biology and other relevant data are not uniformly available for Montiaceae species. Hectorelleae stand out as taxa likely subjected to pollinator scarcity, especially *Lyallia* (Wagstaff & Hennion 2007). Yet their ovule numbers are low by Montiaceae standards. The same is true for several 1–few-seeded *Philippiamra* species of extreme desert habitats. Overall, as with other phenotypic/environmental traits discussed in the present work, pollinator scarcity/unreliability seems to be neither necessary nor sufficient to affect the evolution of ovule number. Ovule numbers among species reflect merely their functional adequacy.

And whatever happened to pollen morphology? The 1960's–1980's were the heyday of palynotaxonomic research, especially because of a then-fashionable newfangled gadget called the electron microscope. The discipline virtually disappeared with the arrival of another fashionable gadget, the PCR machine. In the meantime, Montiaceae and Caryophyllales generally were subjected to numerous palynotaxonomic studies. A few of these include Nilsson (1967), Nowicke & Skvarla (1979), Carolin (1987), and Nowicke (1996). With the advent of molecular phylogenetics, reference to pollen morphology virtually disappeared from the literature.

Montiaceae pollen morphology is considerably diverse. Aperture types include tricolpate, "broad" pantocolpate, "narrow" pantocolpate, and pantoporate (Carolin 1987). All of these forms are shared by other Portulacineae and core Caryophyllales generally (Nowicke & Skvarla 1979, Nowicke 1996), although distinctions might be evident in exine ultrastructure (Nowicke 1996). Generic or subgeneric taxa usually have a single aperture type: Phemerantheae spp. are broad-pantocolpate, Cistantheae spp. are tricolpate except for *Montiopsis* subg. *Montiopsis* spp., which are pantoporate. *Calandrinia* spp. are pantoporate, Hectorelleae and Montieae spp. are tricolpate, except for *Montia* spp., which are narrow-pantocolpate. *Rumicastrum* includes all forms except tricolpate, plus a unique operculate pantoporate form. The individual aperture types phylogenetically are conserved in some subclades of this genus. Thus, aperture type manifests phylogenetic conservation, but also homoplasy. Nilsson (1967) noted the presence of numerous aperture mutants in the normally tricolpate *Claytonia sibirica* L. Tricolpate would seem to be the ancestral form of Montiaceae. The exine surface in Montiaceae pollen mostly is the spinulose-punctate form common throughout core Caryophyllales, but reticulate, psilate, and tholate surfaces occur in particular species.

I do not attempt to explain here Montiaceae pollen evolution and/or its ecological significance. Till-Bottraud et al. (1994) proposed an explanation in the framework of game theory, but I reject this Darwinian Modern Synthesis proposal on epistemological grounds. In fact, I do not propose here evolutionary ecological explanations for any of the variability of Montiaceae

reproductive morphology. I call attention to it here for a different reason. As elaborated below, the modern phylogenetic paradigm tends to focus on the supposed evolutionary consequences of single or a few variable phenotypic/ecological traits, e.g., life history, succulence, ploidy level, ovule number, photosynthetic pathway (see below), temperature/precipitation niche, elevation, or, in general, any trait whose disembodiment and oversimplification thus lends itself to correspondingly simplistic and contrived statistical analysis. Such analyses presume that all other phenotypic traits are "equal." The descriptions of Montiaceae phenotypic/ecological trait variability here serve as a reminder that they are not.

4i. Montiaceae physiological evolution. Current phylogenetic reconstructions indicate that ancestral and early diverging Montiaceae lineages were warm/arid adapted, manifested today by their distribution, succulence, and other phenotypic characteristics. Evolution of Montioideae coincided with a shift to cooler/moisture habitats, hence loss of warm/arid adaptations. However, cool/moist-adapted species also evolved independently in the warm/arid lineages, and warm/arid-adapted species evolved in Montioideae.

Photosynthesis is challenged under warm/arid conditions, in which carbon assimilation via light-dependent ribose bisphosphate carboxylase/oxygenase (Rubisco) becomes water-use inefficient and/or counterproductive. Thus, many warm/arid-adapted plants possess photosynthetic adaptations that permit them to optimize carbon assimilation under these conditions, i.e., C4 and CAM photosynthesis. Both permit carbon assimilation as transitory C4 acids, one carbon then fed into the universal Rubisco C3 assimilation cycle. C4 plants fix carbon efficiently at high temperatures in daylight and shuttle carbon to a physically/mechanically isolated Rubisco cycle. This prevents oxidative photorespiration. CAM plants use the same C4 biochemistry, but they reverse normal light-sensitive stomatal movements, so that carbon assimilation as C4 acid occurs via open stomata at night. The light-dependent Rubisco C3 cycle then functions in daylight with the stomata closed. While C4/CAM terminology is applied in reference to photosynthetic carbon fixation, its biochemical mechanisms exist in all plants and function in other physiological contexts, e.g., in root tissue carbon metabolism. Thus, C4/CAM operation in photosynthesis is coopted/exapted.

Not surprisingly, C4 and CAM species occur among Portulacineae. However, many Portulacineae lineages are not C4 nor obligately CAM, but rather facultatively CAM or "C3-CAM" (Goolsby et al. 2018a, b). C3 assimilation occurs under certain physiological conditions, CAM under others. There exist also C3-C4 intermediates in other Portulacineae. Evidently, many, if not most, Montiaceae are C3-CAM, and none are C4 or obligately CAM (Goolsby et al. 2018a, b). In phylogenetic reconstruction, C3 and C3-CAM transition multiple times throughout Montiaceae evolution. The Montiaceae basal node reconstructs as C3-CAM, the next split as C3, and the *Rumicastrum* ancestor as C3-CAM, with C3 retained as ancestral in all other examined Montioideae genera except *Calandrinia*, whose ancestral state remains ambiguous because phenotypes remain poorly sampled. Within Cistantheae, only the *Cistanthe* ancestor reconstructs as C3-CAM. Perhaps surprisingly, C3-CAM is not demonstrated in *Calyptridium*, although the most arid-adapted species were not studied. *Philippiamra*, which include the most arid-adapted of vascular plants, were not examined. C3-CAM reverts to C3 several times in *Rumicastrum*. Meanwhile, C3-CAM has evolved at least twice in *Claytonia*. Other polytypic genera are inadequately sampled to affirm monomorphism, especially because negative evidence for facultative trait expression may be unreliable.

However, the objective of Goolsby et al. (2018a, b) was to analyze the relationship between evolution of C4/CAM phenotypes and that of metabolically relevant "carbon concentrating mechanism" (CCM) genes. They hypothesized that "positive selection" in these genes should be enhanced relative to other sampled genes of Portulacineae, a lineage that manifests a high rate of C4/CAM/C3-CAM evolution. The premise itself seems to appeal to an arcane (pre-McClintock)

dogma that phenotypic evolution is a linear function of amino acid substitution. Otherwise they would not have considered "surprising" the failure to confirm the hypothesis.

Goolsby et al. (2018a, b) considered possible methodological artifacts that may have affected the results, as well as the possibility that *all* examined genes were under positive selection, but for different reasons. They did not seem to consider the possibility that the CCM genes were already perfectly functionally adequate and/or that factors besides CCM genes affect carbon metabolic expression in vivo. For example, Libik-Konieczny et al. (2019) summarized evidence that the CAM phenotype itself enhances pathogen resistance. This has no direct relation to carbon concentration optimization nor to photosynthetic efficiency in arid habitats or other presumed CAM benefits. Goolsby et al. (2018a, b) did find evidence for convergence at particular Portulacineae CCM gene amino acid sites in C4/CAM species, a result paralleling that for other C4/CAM angiosperms. However, convergence is an observation, not a cause nor an explanation.

4j. Montiaceae phenotypic/ecological evolution and evolutionary epistemology. Hershkovitz (2018c) emphasized the role of epistemology in the interpretation of Montiaceae evolution. Revision of that work will elaborate its thesis further. Hershkovitz (2018c) criticizes the epistemological basis of contemporary comparative evolutionary analysis, epitomized by Ogburn & Edwards (2015), Goolsby et al. (2018a, b), and similar studies. Even if the statistical correlations are accurate mathematically, evolutionary correlation is confounded with evolutionary cause.

Many contemporary comparative evolutionary analyses purport to analyze the phylogenetic causes/consequences of the evolution of single or few biotic characters. The tendency is to idealize phylogenetic parameter space as comprising discrete, independent, and identically distributed taxa, characters, and cladogenetic events. Characters are idealized as having as few discrete and time-reversible states as possible or, alternatively, a continuous linear distribution. These idealizations precisely underwrite the statistical methodology, in which artificially linearized distributions of idealized trait observations are compared with artificially linearized and idealized null distributions. The folly of the approach is evident in analyses such as Ogburn & Edwards (2015), in which nonlinearly related life forms are reduced to two-state life histories, and niche characteristics are proxied using simplistic but easily acquired macroclimate data. Likewise, C3/C4/CAM once was considered a simple three-state characteristic, but its evolution is more complex than its three idealized phenotypes would suggest.

Goolsby (2016; Goolsby et al. 2017) developed rudimentary methods that facilitate simultaneous phylogenetic comparative analysis of multiple parameters. It remains to be demonstrated whether evolutionary analysis of some tractable number of characters can explain adequately the diversification of large clades. Hershkovitz (2018c) argues that it cannot (see below). Alternatively, increasing parameter space may help demonstrate that evolutionary consequences are unpredictable and evolutionary explanations cannot be generalized. In the meantime, no computational advancement can calculate its way around fundamental theoretical and empirical limitations and flaws, many of which have been delineated in previous sections. These include ambiguities in phylogenetic resolution, nonlinearity/nonstationarity of the phylogenetic process, hybridization and lineage sorting, and the behavior of Bayesian estimation when assumptions inevitably are violated. The problem of statistical nonequivalence and nonindependence of taxa also is not addressed.

But irrespective of whether evolutionary correlations appear to be statistically highly significant, Hershkovitz (2018c) rejected the applicability of the probabilistic paradigm to evolutionary analysis (cf. P. Hershkovitz 1977: *64*). Hershkovitz (2018c) traced the roots of the contemporary hegemonic phylogenetic/ phylogenomic paradigm to the Darwinian Modern Synthesis probabilistic population genetics paradigm and its adaptationist notions. In this interpretation,

organismal evolution is conceived as a linear stochastic process, its null trajectory *indeterminate* (i.e., drift) or determined *extrinsically* probabilistically by the interaction of "selective" forces operating at lower (suborganismal) or higher (supraorganismal) hierarchical levels, i.e., traits or environments. In this paradigm, evolution is defined as a statistically significant change in the mean of a trait distribution in a population. Covariation of mean change with some extrinsic parameter evidences "natural selection," evolutionary biology's phlogiston.

Rejection here of Darwin's (1859) Theory of Natural Selection is (NS) far from radical. To the contrary, its rejection is robust and definitive. In particular, preeminent evolutionary theorist Massimo Pigliucci (2010) wrote:

"*…contrary to popular belief, natural selection is not an optimizing process – [which explains] why [natural selection] makes mistakes and is inefficient, yielding whatever outcome is good enough for survival and reproduction.*"

But this characterization is the essence of the non-Darwinian Theory of Natural Drift (Maturana & Mpodozis 2000)! More to the point, it patently *is not* the essence of NS, lest the subtitle of Darwin (1859) would have been "…*The Preservation of 'Good Enough' Races in the Struggle for Life*" or, paraphrased, "*survival of the adequate*" (cf. Darwin 1868). Logically parsed, Pigliucci (2010) implies that natural selection is not selective.

Paradoxically, Pigliucci (2010) made the above assertion in *defense* of NS and criticism of non-Darwinian evolutionary arguments. But, as Hershkovitz (2018c) noted, Pigliucci replaced the Darwinian operational definition of NS with a non-Darwinian one. Hershkovitz (2018c) questioned whether Pigliucci's (2010) gross mischaracterization of NS owed to simple error, speculating instead a political motivation. In particular, acceptance of NS among the world's "educated" citizenry (including the overwhelming majority of nominal scientists) is not scientific, but scientistic. It owes to indoctrination, no different from Creationism or, perhaps more relevant here, Atheism or Marxism. More to the point, societal acceptance of NS has global political and economic consequences.

Meanwhile, acceptance of NS among Modern Synthesis analysts is not logical, but tautological, i.e., NS incarnates in the Price Equation (see Frank 2012; cf. Nespolo 2003). But the hegemonic Modern Synthesis school has a century-long history of condescending to, ridiculing, and even suppressing *both* Creationist *and* non-Darwinian evolutionary ideologies alike (e.g., Nespolo 2003; Lynch 2007). Nespolo (2003) even claimed that teaching of non-Darwinian evolution posed an existential threat to Chilean society. Thus, Hershkovitz (2018c) suggested that Pigliucci's "sleight of hand" attempted to save the face of an arrogant and elitist evolutionary biology institution in the wake of its proselytization of an erroneous theory. Otherwise, the latter potentially undermines society's faith in the public institution of science and its willingness to fund it. On the balance, neither consequence would be necessarily bad for science per se.

The relevance of this discussion here is that the premise of a century of mainstream evolutionary biological literature is wrong, thus invalidating its analyses and interpretations. This applies also to NS-based evolutionary analyses of Portulacineae/Montiaceae cited in this work, e.g., Ogburn & Edwards (2015) and Goolsby et al. (2018a, b). I adopt in this work an apparently more "exotic" non-Darwinian evolutionary perspective. Its merits remain to be corroborated. But, regardless, I maintain that an uncorroborated evolutionary theory cannot be worse than a *wrong* one. Betting on *any* live horse beats betting (and bests beating) on a dead one.

Hershkovitz (2018c) discussed how all biogenetic processes, hence evolution, conform better to formal chaotic than to stochastic functions. Chaotic functions are intrinsically *determinate*, not probabilistic. Seemingly paradoxically, they are *unpredictable*, unless the function and initial

conditions are known. Which, in the case of evolutionary analyses, they are not. This "epiphany" emerged from the conclusion that evolution of Atacama Desert Montiaceae conformed to the evolutionary model of Natural Drift (Maturana and Mpodozis 2000). Indeed, in this model, organismal evolutionary trajectory is unpredictable and determined not extrinsically, but intrinsically, by organismal enactivity itself. Factors at hierarchical levels below and above the organismal level establish initial conditions and bounds for this trajectory, but they do not determine it (cf. Salthe & Matsuno 1995; Yarrow & Salthe 2008; Fábregas-Tejeda &Vergara-Silva 2017).

The preceding observations led Hershkovitz (2018c) to describe the Principle of Evolutionary Idiosyncraticity (PEI), which models organismal evolution as a determinate chaos-like process that is perturbed stochastically by the collective action of myriad forces operating at suborganismal/ supraorganismal levels. [Although inspired by observations of Atacama Desert Montiaceae, PEI actually was conceived and developed while contemplating Chilean horse racing. Horse racing programs document myriad parameters that bettors might use to estimate race outcome probability. In fact, the parameters establish only limiting conditions and bounds, but the race outcome is determined by no more or less than the idiosyncratic enactivity of the horses.]

The principal consequence of PEI is that, if correct, the hegemonic contemporary probabilistic paradigm of comparative evolutionary analysis is scientifically invalid. Hershkovitz (2018c) provides independently derived conclusions to this effect (e.g., Wenzel & Carpenter 1994; Franz & Engels 2010). A conundrum appears to arise to the degree that scientific conclusions obligate probabilistic analysis. This proves to be a red herring. Hershkovitz (2018c) suggested that, while the outcome of a chaotic process is unpredictable statistically, it should be statistically differentiable from that of any stochastic process. Thus, Hershkovitz (2018c) suggested that this can be accomplished by inverting null hypotheses.

For example, Goolsby et al. (2018a, b) explicitly state that their failure to reject the null hypothesis of relative neutrality of CCM gene evolution was "contrary to expectations." The objective of science must be to challenge and not affirm expectations. As "positive selection" clearly is the expectation, it should be the null hypothesis tested. I suspect that invariably it would be rejected. Repeated rejections in specific cases eventually would lead to rejection of positive selection theory generally and a search for a better theory. Hershkovitz (2018c) intimated that most or all of contemporary evolutionary biological dogma would not withstand proper statistical scrutiny.

Hershkovitz (2018c) noted, moreover, that empirical evidence from Montiaceae already implicates nonstochasticity of evolution. In particular, the genus *Lewisiopsis* possesses the growth form, cytological traits (octaploid), evolutionary history (evidently a hybrid), and geographic range (western North America) that, individually, have been predicated to promote phylogenetic and ecological diversification. Yet, the monotypic genus evidently is an isolated relict, morphologically and genomically similar to its Eocene ancestors. This might be interpreted statistically as a "longshot," but PEI explains the outcome as determined intrinsically by the organisms and not by any particular trait or circumstance.

5. Montiaceae Historical Biogeography

5a. Phylogeographic disjunctions among Montiaceae. The native range of Montiaceae includes NE Siberia, the Americas, especially along the cordillera, from Alaska to Tierra del Fuego, Australia, New Zealand, and the Kerguelen Islands. One species, *Montia fontana*, is cosmopolitan in temperate and cool tropical habitats. Hershkovitz (2018a, b) reviewed evidence for Montiaceae phylogeographic history, and a revision of that work will elaborate further on its theses. The principal conclusion was that all transoceanic and perhaps even many terrestrial disjunctions among Montiaceae taxa originated via long distance dispersal (LDD) and not vicariance.

Below is a list of Montiaceae phylogeographic disjunctions of 1000 km or more, both transoceanic and terrestrial. Likely anthropogenically-induced disjunctions are excluded. I attribute all trans-oceanic disjunctions to LDD and terrestrial ones at least plausibly so.

1. *Schreiteria* (S Am) - *Phemeranthus* root (N Am or C Am)

2. *Phemeranthus* root (N Am or C Am) - *P. punae* (R.E. Fr.) Eggli & Nyffeler (S Am)

3. *Phemeranthus spinescens* (Torr.) Hershk. and *P. sediformis* (Poelln.) Kiger (Pacific NW N Am) - remainder of *Phemeranthus* (N Am, > 1000 km E and S)

4. *Cistanthe* clade (S Am) - *C. guadalupensis* (T.R. Dudley) Carolin ex Hershk. & *C. maritima* (Nutt.) Carolin ex Hershk. (N Am)

5. *Philippiamra* (S Am) – *Calyptridium*/*Thingia* (N Am; phylogenetic evidence does not establish whether this represents one disjunction or two)

6. Montioideae root (S Am) - *Rumicastrum* (Aus)

7. *Calandrinia acaulis* Kunth (S Am) - *C. acaulis* (C Am)

8. *Calandrinia ciliata* (Ruiz & Pav.) DC (S Am) - *C. ciliata* (C Am)

9. *Calandrinia* sect. *Calandrinia* (S Am, C Am) - *C. menziesii* (Hook.) Torr. & A. Gray (N Am)

10. *Calandrinia* sect. *Calandrinia* (S Am, C Am) - *C. bonarensis* Hauman (Buenos Aires Province, ARG; this species currently is identified as *C. ciliata*, but the disjunction exists either way)

11. Montioideae root (S Am) - Hectorelleae (NZ, Kerguelan I)

12. *Hectorella* (NZ) - *Lyallia* (Kerguelan I)

13. Montioideae root (S Am) - Montieae root (N Am)

14. *Lewisia pygmaea* s. l. (lower USA, S Can) - *L. pygmaea* s. l. (N Can, Alaska)

15. *Claytonia* sect. *Claytonia* spp.(lower USA) - *C. ogilviensis* McNeill (Yukon; see Stoughton et al. 2017a)

16. *Montia* root (N Am.) - *Montia* sect. *Australiensis* (NZ, Aus.)

17. *Montia* sect. *Australiensis* (NZ) - *M.* sect. *Australiensis* (Aus)

18. *Montia* sect. *Australiensis* root (NZ or Aus) – *M. howellii* S. Watson (N Am; not anthropogenic contra O'Quinn et al. 2005; see Hershkovitz 2018a, b; see also Mason 1934; cf. Axelrod 1983)

19. *Montia* sect. *Montia* root (N Am) - *M. meridiensis* Friedrich (S Am)

20. *Montia fontana* root (N Am) - *M. fontana* (subcosmopolitan, pre-anthropogenic)

21. *Montia chamissoi* (Ledeb. ex Spreng.) Greene (N Mex - Alaska) - *M. chamissoi* (S Mex)

5b. Evidence for pre-Columbian anthropogenic Montiaceae dispersal. I classify the preceding disjunctions as non-anthropogenic. More accurately, in the case of Western Hemisphere Montiaceae and plants in general, I refer to human dispersal beginning in the age of transoceanic global exploration and settlement, ca. 1500 AD and thereafter. Without doubt, massive transoceanic travel initiated the catastrophic phase of the global biotic diaspora. However, anthropogenic dispersals since the dawn of the human evolution have had significant consequences on modern taxon ranges and genetics. This is evidenced in the pre-colonial Western Hemisphere, especially in the case of cultivated taxa (Piperno 2011). But, just as in SW Asia and Europe, presumably New World indigenous migration over several millennia would have influenced also at least passively the distribution especially of useful non-cultivated and weedy plants.

Archeological and anthropological evidence indicates that pre-Columbian migrations may have affected the distribution especially of certain North American *Calandrinia*, *Claytonia*, and *Lewisia* spp., though there is no specific evidence involving South American Montiaceae. However, the evidence does not undermine the thesis that non-anthropogenic LDD explains most major Montiaceae disjunctions.

The most tangible evidence for anthropogenic range intervention among Montiaceae involves the bitterroot plant, *Lewisia rediviva* Pursh. This is considered to have been an important food and medicinal plant in pre-colonial western North America (Bandringa 1999; Davidson 2000). Assuming that the *L. pygmaea* complex is polyphyletic (see below), *L. rediviva* has the most expansive range of any *Lewisia* species (Hershkovitz & Hogan 2003) and among the more expansive among all Montiaceae. Bandringa (1999) described in detail the indigenous people's harvesting of natural populations in Alberta, Canada, and sometimes successful transplanting/cultivation attempts. Wilson et al. (1988) believed that transplantation expanded the range of the species. However, Strong et al. (2003) believed that Hypsithermal warming, ca. 6000–9000 years before present (ybp), explained this and other latitudinal disjunctions in northern North America. But they conceded that LDD and anthropogenic dispersal could not be ruled out. Regardless, the bitterroot harvesting process itself likely transported seed. The limited interfertility among the *Lewisia* spp. (Mathew 1989; Davidson 2000) renders a possibility that anthropogenic dispersal of *L rediviva* may have facilitated gene flow between this and other more range-restricted species.

California indigenous peoples harvested large quantities of the edible seed of the native *Calandrinia menziesii* and/or *C. breweri* S. Watson (Timbrook et al. 1982, Bousman et al. 2012, Reddy 2014). The seeds were stored in large earthen jars and sometimes ceremonially buried. It is not clear whether the plants actually were cultivated, but any degree of deliberate or accidental transport would be sufficient to establish new populations. *Calandrinia menziesii* is especially weedy in California and broadly distributed between Arizona and S British Columbia. Again, Hypsithermal warming might explain the latitudinal distribution (Strong et al. 2003), but other mechanisms cannot be ruled out. The species is human-introduced in Australia, New Zealand, and the Falkland Islands.

The genetically, but apparently not morphologically, distinct species *Calandrinia ciliata* (Hershkovitz 2006), is an important non-cultivated harvested leaf vegetable in Mexico ("chivito;" Castro Lara et al. 2011). This suggests a possibility that the California/Mexico connection might be anthropogenic, but circumstantial evidence is not corroborative. The California plants are a seed crop used by a lowland/coastal culture and, indeed, the California plants flower/seed prolifically. The Mexico plants are a leaf crop used by a montane culture and evidently flower/seed more reservedly. The latter I have surmised on the basis of herbarium collections and numerous internet images of Mexican *C. ciliata*, in herbaria, growing, or in markets. In addition, *Calandrinia menziesii* reportedly was present in California during the Pleistocene, ca. 28,000 ybp (Mason 1934; cf. Axelrod, 1983).

Several *Claytonia* species also were used as food by indigenous peoples (Miller & Chambers 2007; Native American Ethnobotany Database 2019). Among these is the widespread and weedy *Claytonia perfoliata* complex, commonly known as "miner's lettuce," whose leaves are eaten raw or cooked. Roots/tubers of several species of *Claytonia* sect. *Claytonia* were eaten (Miller & Chambers 2007), and cultivation likely was attempted (Bandringa 1999). Again, even passive anthropogenic dispersal would be sufficient to perturb local gene pools and create some of the taxonomic havoc (Stoughton 2017a, b) in this group.

There is less evidence for anthropogenic dispersal of South American Montiaceae. Many other cultivated species were dispersed anthropogenically between Central and South America along the cordillera by indigenous highland peoples (Piperno 2011). This reflects continuity of the distinctive cordilleran climate and physiognomy, and the development of a corresponding agronomic culture distinct from a forest or coastal culture. But the South American cordillera also circumscribes a natural biogeographic corridor, so natural versus anthropogenic biotic movements during the past ten millennia would be difficult to discern.

South American Montiaceae evidently had little ethnobotanical importance. Unlike important Andean crop species, it is unlikely that their natural ranges were perturbed deliberately. *Calandrinia compressa*, like *C. ciliata*, evidently was a minor leaf vegetable. Multiple internet sources provide a common name, "vinagrillo," which, like "chivito," refer to its acidic flavor. Vinagrillo evidently is an ethnobotanical "genus," as it also is applied to *Oxalis* spp., which, like *Calandrinia* spp., contain considerable oxalic acid. High elevation perennial *Calandrinia* spp. were used for livestock foraging (Aldunate et al. 1981; Jai Vidaurre 2006). *Cistanthe* spp. reportedly had medicinal applications analogous to similarly succulent and mucilaginous aloes (Aldunate et al. 1981; Cecchini & Ticli 2016). Bahamondes et al. (2012) reported that leaves of *Cistanthe* spp. (including *Philippiamra* spp.?) afforded solar/heat protection to indigenous desert travelers. Obviously, using plants as sportswear afford an opportunity for anthropogenic dispersal.

An anthropogenic intervention in Andean Montiaceae diversification would have been passive. Such is not unlikely, however. Many Montiaceae have weedy tendencies, and, indeed, certain Chilean species of *Calandrinia*, *Cistanthe*, and *Montiopsis* are especially abundant on disturbed sites, especially along roads and in cultivated fields. It seems unlikely that human migrations in the Chilean region over the course of ten millennia never would have dispersed any Montiaceae species to new sites, and also facilitated gene flow among populations and interfertile species. However, distinguishing between such anthropogenic and non-anthropogenic effects would be difficult, if not impossible.

5c. Evidence for Montiaceae age and metastasis. Montiaceae origins/diversification are not preserved in the fossil record (Hershkovitz & Zimmer 2000). Evidence for their age and metastasis is circumstantial, although molecular dating evidence offers a degree of tangibility. Based on what were considered then typical rates of ITS substitution in herbaceous lineages, Hershkovitz & Zimmer (1997) estimated that Montiaceae originated 8–16 million years before present (mybp). They noted that an age of 80 mybp would follow from rates estimated for long-lived trees. These substitution rates had been estimated for other taxa using one or another sort of calibration point. Using a tree-based approach calibrated by Hawaiian island ages, Ocampo & Columbus (2012) estimated Montiaceae age at 13 mybp, which seemed to corroborate Hershkovitz & Zimmer (2000).

However, all subsequent fossil-calibrated tree-based age estimates that sampled Caryophyllales more broadly are much older. Ogburn and Edwards (2015) and Hancock et al. (2018) dated Montiaceae origins at, respectively, ca. 34 and ca. 43 mybp, i.e., late Eocene to perhaps earliest Oligocene. These estimates do not significantly alter the phylogeographic conclusions of Hershkovitz and Zimmer (2000) with respect to LDD. At the same time, all tree-based estimates indicated that

diversification of modern species occurred from the Miocene and mostly the Pliocene onwards, much more recently than major lineage origins. However, I speculated above and in Hershkovitz (2006) how molecular markers might underestimate the true age of generic-level diversification among Montiaceae. These ideas must be kept in mind in the following discussion.

The most recent Caryophyllales molecular age analyses (Yao et al. 2019) date Portulacineae and Montiaceae crown divergences at ca. 75 and ca. 60 mybp, respectively. They estimated the Portulacineae-Molluginaceae split at ca. 85 mybp. The authors estimated similar ages for crown divergence of several families throughout Caryophyllales, and argued that this corroborates evidence for massive early Paleogene diversification following Cretaceous mass extinctions. These older estimates affect significantly the phylogeographic interpretation of Montiaceae, as it renders more plausible vicariance of the earliest divergences.

Aligning the 34–43 mybp age estimates with paleoclimatic evidence and the overall phylogenetic trend towards cooler /moister habitats described above, Hershkovitz (2018a, b) proposed that the early diverging arid-adapted Montiaceae lineages Phemerantheae, Cistantheae, and *Rumicastrum* originated in west-central South America during the late Eocene (but see discussion of *Phemeranthus* below). Aridity in this region had established as early as the Jurassic (Hershkovitz et al. 2006a). But both hyperarid and alpine taxa in these first two lineages originated much later with the development of these habitats in, respectively, North America and South America. Given the low genetic divergence within the relevant genera (Hershkovitz 2006; Price 2012), this diversification likely occurred rather recently, perhaps Pliocene (but see below).

Hershkovitz (2018b) suggested that the ancestor of cooler-adapted Montioideae (*Calandrinia*, Hectorelleae, and Montieae) was situated in southern Patagonia during the Oligocene. Both annual and perennial *Calandrinia* taxa spread northward along the uplifting Andes, eventually arriving in Central America and North America via LDD. This presumes that there was never a suitably cool terrestrial connection between the continents. Even so, given the evidential propensity for LDD, the transitory existence of a terrestrial migratory route does not necessarily favor the vicariance hypothesis (see below). Likewise, it is not clear whether the annual *Calandrinia* species of the western US arrived (overland or via LDD) from the most proximal source in Mexico or represent an independent LDD from South America. Meanwhile, Hectorelleae migrated to New Zealand (and/or the Kerguelen Islands) directly or via Antarctica. The Montieae ancestor migrated via LDD to temperate North America.

The 34–43 mybp Montiaceae age estimates remain consistent with Hershkovitz & Zimmer's (1997, 2000) conclusion that the many intercontinental/interoceanic disjunctions among Montiaceae and other Portulacineae owe to LDD. This conclusion is consistent with that speculated on the basis of non-cladistic taxonomy (Raven and Axelrod 1974). The result is significant in that Montiaceae generally have no obvious morphological specialization to facilitate long distance dispersal via zoochory or anemochory. Most *Cistanthe* species are excepted, because their seeds have a short and somewhat sticky pubescence that facilitates passive zoochory. But *Cistanthe* account for only one Montiaceae intercontinental disjunction. Seeds of some *Phemeranthus* spp. have a membranous exotesta (pellicle; Price 2012), and strophioles occur in several genera, but the utility of these in LDD is not confirmed. Some Portulacineae (e.g., Basellaceae, Cactaceae, and *Talinella*) have fleshy fruits, but other taxa, e.g., *Portulaca*, have no obvious LDD mechanism. The pan(sub-)tropical distribution of *Portulaca* has been attributed to LDD (Ocampo & Columbus 2012).

Other researchers (e.g., Carolin 1987; Applequist & Wallace 2001; but see Applequist et al. 2007; cf. Moreira Muñoz 2011: 216) have explained at least intergeneric Portulacineae distributions in terms of vicariance resulting from the break-up of Gondwana. Some distributional patterns render appealing such explanation, especially African endemism of Didiereaceae. The older divergence

dates estimated by Yao et al. (2019) seem to lend some credence to the notion that the oldest intercontinental disjunctions among Portulacineae could owe to vicariance. Older Montiaceae disjunctions could also, but I still doubt it (see below).

An intriguing aspect of the 75 mybp estimate for the Montiaceae split is the reconstructed geography of the western hemisphere during the late Cretaceous (Scotese 2017). At that time, the western American cordilleran region was somewhat disjoint from eastern Laurasia. In North America, the cordilleran region was separated by an interior sea that extended south to include much of Mexico and Central America. And it was closer to South America than it is today. At the same time, the central Andes region formed a peninsula whose arc aligned with the southern end of Central America. A further intriguing observation is that, according to Yao et al.'s (2019) estimate, the split between largely North American *Phemeranthus* and remaining largely South American Montiaceae occurred at ca. 65 mybp (see also below). Thus, the scenario is somewhat suggestive of a late Cretaceous land bridge. Humphries and Parenti (1986, 1999) had proposed that a land bridge explained the repeated pattern of western American antitropical disjunctions (see also below).

While the Yao et al. (2019) chronogram (if correct) would be consistent with a larger role for vicariance in Portulacineae and Montiaceae phylogeographic history, most Portulacineae (including Montiaceae) disjunctions still appear to be too recent to involve vicariance. For example, the chronogram would date the *Rumicastrum*-Montioideae split to ca. 55 mybp. Divergence at this and subsequent nodes largely is responsible for the more "cosmopolitan" distribution of Montiaceae, i.e., phylogenetically successively, *Rumicastrum* in Australia, *Calandrinia* mainly in South America, Hectorelleae in New Zealand and the Kerguelen Islands, and Montieae in North America.

Hancock et al. (2018) suggested that *Rumicastrum* could have arrived from South America vicariously, which would have been highly unlikely given their own divergence age estimate (Hershkovitz 2018b). The Yao et al. (2019) estimate coincides with the separation of South America and Antarctica (Livermore et al. 2007), such that a proto-*Rumicastrum* conceivably could have spanned southern Gondwana terrestrially. However, at ca. 50 mybp, the span from S Patagonia to Australia was cooler and wetter than the ancestral Montiaceae range in NW Patagonia. A vicariance scenario implies that proto-*Rumicastrum* evolved from a warm/arid-adapted ancestor, but was itself more cool/moist-adapted.

Hancock et al. (2018) estimated that the ancestral area of *Rumicastrum* is (currently) warm/arid western Australia, but they also noted that this climate developed in the Miocene. This means that proto-*Rumicastrum* indeed might have been cooler-adapted, which implies that the warm/arid adaptation of *Rumicastrum* is convergent on the ancestral Montiaceae condition. And adaptation of *Rumicastrum* spp. to cooler and moister habitats occurred yet again as species evolved into northern, southern, and eastern Australia. However, Goolsby et al. (2018a, b) reconstructed the *Rumicastrum* ancestral node as C3-CAM, which suggests warm/arid adaptation. There is no empirical evidence for a cool/moist-adapted *Rumicastrum* ancestor, but inference of "unseen" ancestral transformations is not unprecedented, e.g., Hershkovitz et al. (2006a). Possibly empirical evidence will emerge from detailed genomic comparison. In the meantime, the *Rumicastrum* age estimate discrepancy, the ancestral phenotype, and the mode of arrival to Australia require additional investigation.

Although Yao et al.'s (2009) chronogram does not include *Calandrinia* or Hectorelleae, extrapolation would place their age at ca. 50 mybp, well after the South America separation. Even if present in Antarctica at that time, vicarious arrival of Hectorelleae to New Zealand and the Kerguelen Islands still seems doubtful, especially because the taxa evidently grow and migrate extremely slowly (Hershkovitz 2018b). Divergence of Montieae as early as 50 mybp still cannot explain their North American distribution by vicariance. Finally, most of Montiaceae disjunctions involve relatively

recently diverged species. This is a point emphasized below: if most Montiaceae disjunctions are too recent to be explained by vicariance, why, especially in the absence of fossil evidence, is vicariance a preferred explanation for the older ones?

At the same time, the discrepancy between the age estimates of Yao et al. (2019) and those of Hancock et al. (2018) and earlier workers beg reconciliation. At the time of this writing, Yao et al. (2019) is not published formally and their data are not available for scrutiny. And molecular dating methods are subject to and incorporate the very same sorts of artifacts as molecular phylogenetic reconstruction generally (see above and Hershkovitz 2018b).

A more trivial geographic aspect of Montiaceae geographic origins relates to Chile. The first phylogenetic divergence separates Phemerantheae from the remainder of the family. The next divergence separates largely Chilean Cistantheae from *Rumicastrum* and Montioideae, and the first split in the latter separates largely Chilean *Calandrinia*. Thus, excluding Phemerantheae, the origin of the rest of Montiaceae appears to have occurred in present day northern Chile. There, it diversified mostly southwards, many descendents dispersing to other lands and diversifying, dispersing, and diversifying further. This appears to be the only intercontinentally diversified plant lineage that originated in present day Chile.

In fact, Chile is known for its high phytogeographic endemism (Moreira Muñoz 2011), indicating that this region has been mainly a phytogeographic sink and not a source. Hershkovitz (2018b) speculated that this may owe to Chile's narrow longitudinal breadth, high relief, and, most of all, historical ecological instability. This may result in high lineage extinction rates, which, in turn, offer more opportunities for colonization. Montiaceae, in turn, are among the few lineages that not only diversified under these circumstances, but evolved their own global colonization capability.

However, the basal split between trans-cordilleran Phemerantheae and cis-cordilleran Montiaceae presents a phylogeographic puzzle. Given the morphological and ecophysiological similarities of *Phemeranthus* and other trans-cordilleran Portulacineae to Cistantheae, why are there not more Portulacineae lineages in Chile? Possibly the question is artificial, as various Cactaceae entered Chile at many different times, presumably since the Miocene (Nyffeler & Eggli 2010b; Moreira Muñoz 2011). However, the other trans-cordilleran taxa, Anacampserotaceae, Basellaceae, and Talinaceae, besides Phemerantheae, are absent in Chile, and only one species of Portulacaceae is native to Chile (Moreira Muñoz 2011).

The cordilleran partitioning of Portulacineae is characteristic of many angiosperm lineages (Luebert & Weigend 2014). Based on present geography, it is tempting to believe that the Andes themselves formed a physical barrier and/or created an indirect ecological barrier against trans-Andean migration (Luebert & Weigend 2014). But popular theory maintains that half or more of the modern height of the central and southern Andes was uplifted relatively rapidly beginning in the Miocene. Before that, the trans-Andean macroecological contrast was less marked and abrupt.

Also, the modern Mediterranean and hyperarid climates are considered to have developed even more recently (Moreira Muñoz 2011). But current estimates place the basal split of Montiaceae in the late Eocene, perhaps 25 million years before the physical/macroecological partition and contrasts developed. Unless the much younger age estimates of Hershkovitz & Zimmer (2000) prove to be correct, the Andes cannot explain the phylogeographic partition. However, some evidence indicates that significant cordilleran height indeed was achieved by the Oligocene (Luebert & Weigend 2014). More recent interpretations of the Andes uplift are nuanced (e.g., Armijo et al. 2015; Quade et al. 2015; Lease et al. 2016; Rodríguez Tribaldo et al. 2017) and do not entirely resolve the question of when the Andes became a phytogeographic barrier.

Among other possible explanations for the phylogeographic partition of Portulacineae in Chile is prior broader cis-cordilleran distribution of currently trans-cordilleran taxa, followed by extinction caused by the drastic changes in climate and/or topography. However, it is not established that the absent trans-cordilleran lineages ever occurred in Chile. Another possibility is that South American cis-cordilleran Montiaceae themselves originated from an ancestor dispersed from North America. The putative phylogeography of *Phemeranthus* (Price 2012; see also Ocampo & Columbus 2012) renders plausible this scenario. As noted above and in Hershkovitz (2018b), the historical ecological instability combined with relatively small geographic area of Chile itself renders its vulnerability to colonization, possibly explaining the tendency of Chile to have become a phylogeographic sink rather than source.

Phylogeny within *Phemeranthus* itself presents a phylogeographic enigma. A basal split separates two clades, and the basal split of each clade defines a major geographic disjunction (Price 2012; cf. Hershkovitz & Zimmer 2000). One clade includes the South American *P. punae* and a small clade of largely Mexican species. The other includes the two Pacific NW US species and a disjunct clade comprising the remaining species, which are distributed >1000 km to the east and south in the central, S, SW, and SE US and northern Mexico. Based on Hershkovitz & Zimmer (2000) and Ocampo & Columbus (2012), Price (2012) presumed a Miocene age for *Phemeranthus* divergence (ca. 13 mybp; see above) and correspondingly more recent ages for these disjunctions. Obviously, the three different older *Phemeranthus* age estimates (respectively, ca. 34, 43, and 60 mybp; see above) would implicate different biogeographic scenarios.

In summary, Montiaceae geographic origins, age, and metastasis remain challenging problems to resolve. The working hypothesis advanced here involves origins in west central South America followed by LDD of ancestors of what became major lineages on other continents, and thereafter continued intercontinental LDD and terrestrial metastasis via migration or LDD. Some evidence is consistent with alternative scenarios of origin and early metastasis, but there seems little evidence countering a significant role of LDD within genera. Much of the resolution rests upon the phylogenetic chronology. None of the age estimates proposed to date are inherently unreasonable. But they are "all over the place" with respect to the actual timing of phylogenetic events.

5d. Montiaceae biogeography and biogeographic epistemology. The preceding accounting of Montiaceae historical biogeography is unapologetically a single-taxon narrative. The synthesis is elaborated much like classical taxon-specific phylogeographic narratives, but incorporates cladistic epistemology and molecular divergence-based estimates of taxon ages (such as they are), as well as other epistemological considerations. Both narrative and taxon-specific analysis might be anathema to method- and/or ideologically-oriented biogeographers (Moreira Muñoz: *Ch.* 10). But, in the end, the objective of all approaches ultimately is a narrative. Some evidence presented here indeed was derived methodologically (O'Quinn et al. 2005; Ocampo & Columbus 2012; Price 2012; Hancock et al. 2018), but the methods and their application were not analyzed here critically.

Epistemology and methodology influence interpretation of Montiaceae biogeography, for which reason I elaborate on the theme here. The view taken here is that the number and complexity of parameters, quantity of unknown data, and precariousness of methodological assumptions restrict to heuristics the utility of "objective" computational phylogeography. No attempt is made here to summarize, much less critically review, the myriad philosophies and/or methods conceived and/or implemented during past two decades or so. An eclectic list of references give some idea of the philosophical polemic and parametric complexity: Nathan (2006; Nathan et al. 2008), Upchurch (2008), Heads (2009, 2014), Wallis & Trewick (2009), Crisp et al. (2011), Moreira Muñoz (2011), Ronquist & Sanmartin (2011), Wiley & Lieberman (2011), Gillespie et al. (2012), Matzke (2013), Warren et al. (2014), and Ebach et al. (2017). In addition, molecular dating has spawned a new paradigm, genomic geochronology (Baker et al. 2014). Here, the chronological alignment of cladistic

events is used to discover/corroborate paleogeological/paleoclimatological events. This approach underlies the thesis that Montiaceae and other Caryophyllales families originated/diversified coincident with the Cretaceous-Paleogene boundary (Yao et al. 2019).

The challenge of phylogeography can be understood in terms of the parametric complexity of its biotic and abiotic components. Biotic components include taxonomy, spatiotemporal phylogeny, and essentially all components of the biology of organisms. Abiotic components include all aspects of neo- and paleo- geology and climatology, as well as spatial relations (i.e., geography). The two components intersect in neo- and paleo- ecology. Much of the present treatise emphasizes that the complexity of biotic components proscribes analytical simplisticity. But, as Moreira Muñoz (2011: *Ch. 10*) emphasized, the abiotic complement is no less important. Systematists tend to be (at best) more critically analytical of biotic evidence and less of abiotic. They tend to cite geological and climatological dogma uncritically as established fact. This is equivalent to geologists and climatologists uncritically citing taxonomy in a most recent popular floristic reference, e.g., Reiche (1898) in the case of Chilean Montiaceae. So, Moreira Muñoz' point must be well-taken. But a biotic bias in phylogeographic interpretation is justifiable, as concluded below.

The legitimacy of the taxon-specific narrative approach adopted here lies in its flexibility and nonlinearity, in particular its capacity to incorporate singular *nuance*. The present work describes amply the limitation of global quantitative evolutionary analysis that disregards nuance. Examples include statistical nonequivalence of operational taxa, nonstationarity of estimated molecular evolutionary "rates," concomitant order of magnitude differences in estimates of cladistic chronology, and the effect of simplistic global parameterization of plant traits such as life history and ploidy, as well as niche traits. Quantitative historical biogeographical methods inherit these shortcomings and add several parametric dimensions of their own. These include arbitrary and dubious definitions of "areas." Thus, as much or more than described in previous sections, quantitative historical phylogeographic analysis intrinsically is inconsistent: the more taxa and areas added, the more violated become the simplistic assumptions.

a. *Biogeography top-down or bottom-up?* A more existential debate in historical phylogeography concerns the hierarchical level to which the science pertains. Some researchers evidently or explicitly prefer a top-down approach that searches for the most-to-least inclusive biogeographic regions/patterns evident from higher to lower taxonomic levels. The approach seeks to explain lower level biogeographic incidence in terms of higher level biogeographic cause. The approach adopted here is phylogenetically bottom-up, whereby broader biogeographic patterns emerge (or not) from the sum of parts and have multiple and sequential historical causes. The debate is analogous and probably psychologically equivalent to the Clement/Gleason ("socialist"/"capitalist") polemic on the tangibility of ecology communities.

The present discussion of Montiaceae phylogeography uses phylogenetic evidence to both discover and challenge phylogeographic hypotheses, including those emergent from the top-down paradigm. In fact, this approach was applied in my earliest Portulacineae research (Hershkovitz 1991), yielding diagnosis of the Western American (slash Australasian) and Eastern American/African groups. However, these informal groupings were taxonomic and not per se biogeographic. Their names merely described the areas of predominant diversity and presumed diversification. But each group had species in the alternate area. The Western American group ultimately became Montiaceae, the basal divergence of which separated the biogeographically intermediate *Phemeranthus*. The last is the only nominally "eastern American/African," lineage of Montiaceae, but it is restricted to America and absent in Africa.

Epistemologically and methodologically, the top-down approach incarnates in chorology (e.g., Moreira Muñoz 2011), panbiogeography (e.g., Heads 2014), and, essentially, in the original

vicariance biogeography paradigm (e.g., Humphries & Parenti 1986, 1999). These approaches presume that patterns represent tangible and/or historical entities/processes. They therefore subordinate taxon-specific narratives to pattern discovery. Chorology divides regional biodiversity among groupings (provinces, regions, or "elements" in Moreira Muñoz 2011) based on taxonomic distinctiveness and/or similarities with other regions. This creates a biogeographic map "deconstructed" from the physical geographic map (Moreira Muñoz 2011). But it is achronological, viz., it is agnostic towards historical biotic assembly.

Panbiogeographical "tracks" are similar to chorological elements in emphasizing interregional taxonomic similarity, but "tracks" purport to be both historical geographic and phyletic hypothesis. Vicariance biogeography emerged with a panbiogeographic mindset on the nature of past geographic connections between disjunct taxa. It departed from panbiogeography in deriving area cladograms as a function of taxon phylogenies derived independently according to cladistic epistemology. Cladistic epistemology effectively is rejected in panbiogeography. In the latter, the most parsimonious phyletic hypothesis is the one that best explains (purported) geographic relations (e.g., Heads 2014; see also below). More recent derivatives of vicariance biogeography (see Ronquist & Lieberman 2011) increasingly emphasized taxon-specific cladistic criteria, avoid ad hoc assumptions on the significance of regional geographical taxonomic similarities, and have become more agnostic towards a priori assumptions of historical geographic relations.

Note that panbiogeography and chorology (more or less) are comparable to clique methods in phylogenetics. In particular, both approaches diagnose biogeographical entities (elements or tracks) as cliques that optimize the distribution of taxa (as traits) among areas. This approach is inherent to an epistemology that predicates that large numbers modern disjunct distributions are borne of fewer ancient continuous ranges. Patterns thus are geographic "symplesiomorphies." This contrasts cladistic epistemology, which diagnoses evolutionary entities based on historically shared evolutionary transitions. Thus, shared distributions can reflect both ancient and recent events.

Moreira Munoz (2011) presented a chorological/panbiogeographic classification of the Chilean flora, which includes seven Montiaceae genera. The work is illustrative of artifacts inherent to the chorological approach. Apparently following Moreira Muñoz & Muñoz Schick (2007), the author classified genera present in Chile into seven floristic elements, some subdivided into generalized panbiogeographic tracks, thus yielding a total of 10 biogeographic entities. Moreira Muñoz did not justify analysis at the generic level. Presumably genera optimize both ease of data gathering and number of inter-area similarities/contrasts. But obviously generic splitting/lumping would (and does) affect the chorological analysis, as does evidence from phylogenetic levels both above and below the generic level (see below). Unless I missed it, Moreira Muñoz (2011) and Moreira Muñoz & Muñoz Schick (2007) did not articulate analytical methods for deriving their floristic elements or tracks or for classifying genera into them.

Moreira Muñoz' (2011) analysis is purely spatial and does not incorporate evidence for phylogenetic chronology. As an example, he delimited an australasiatic floristic element comprising genera shared between Chile and Australasia whose distribution "can be traced to the Gondwana era, as a once-continuous cool-temperate flora, now scattered into a relict distribution by tectonic movements" (Moreira Muñoz 2011: *92–93*). He divided this element into three generalized tracks: austral-arctic, circum-austral, and tropical Pacific, depending upon whether a genus also includes species in, respectively, southern Africa or tropical Australasia.

In his "tropical Australasian track," Moreira Muñoz (2011) included the taxonomically problematic *Hebe* (Plantaginaceae). *Hebe* in its broadest sense segregates most Australasian species of the consequently paraphyletic genus *Veronica* (Wagstaff et al. 2002; Albach et al. 2005; Albach & Meudt 2010). In the strictest circumscription, *Hebe* does not occur in the tropics, thus has no

"tropical" track. In the broadest circumscription, *Veronica*, with *Hebe* included, is cosmopolitan. Here we see the problem of biogeographic analysis at arbitrary taxonomic levels.

Two species of *Hebe* (s. str., s. l., or as *Veronica*) each occur in both New Zealand and southern Patagonia. Genetic divergence between disjunct samples is low. Thus, based on genetic and morphological *evidence*, the presence of *Hebe* in *both* Patagonia *and* Australasia has been explained as LDD (Wagstaff et al. 2002; Albach et al. 2005; Albach & Meudt 2010; cf. Winkworth et al. 2002, Wallace & Trewick 2009). (Negative) fossil evidence corroborates this conclusion. The only *evidence* that these disjunct distributions represent relictual vicariance is that Gondwana once existed. Moreira Muñoz (2011) separately addressed the LDD/vicariance polemic generally (see below) and described evidence for a few taxa, but not *Hebe*.

In any case, Moreira Munoz´ (2011) chorological/panbiogeographic categories would seem to corroborate/validate themselves only on the basis of the number of taxa they contain, without elaborating evidence whether the shared distributions of included taxa are homologous or convergent. Alternatively, Moreira Muñoz' (2011) track classification of *Hebe* may betray his uncorroborated conclusion that these two disjunct modern species of *Hebe* existed and spanned Gondwana in the earliest Eocene. These perspectives are critical to interpret the associated classification of Montiaceae.

Setting aside the cosmopolitan *Montia fontana*, Moreira Muñoz (2011) assigned Chilean autochthonous Montiaceae genera to two floristic elements and a total of three tracks: Neotropical - Central Andean track (*Montiopsis*); Neotropical - Wide Neotropical track (*Calandrinia*); and Antitropical - Pacific track (*Cistanthe*; sensu Hershkovitz 1991, including *Philippiamra*, evidently overlooking Hershkovitz 2006). *Lenzia* was classified in the Neotropical element, but, being monotypic, no track is assigned, as though it generated spontaneously and has no biogeographical relations. Moreira Muñoz (2011) characterized the Wide Neotropical track genera as having diversity concentrated mainly in the intertropics. The Central Andean and Antitropical elements localize at, respectively, tropical and temperate latitudes.

Montiaceae distributions in Chile reveal the limitations of the chorological approach, and this evidently extends to other taxa. Multiple species of *Calandrinia, Cistanthe, Philippiamra*, and *Montiopsis* extend into tropical Southern latitudes in nightly/seasonally cool/cold (i.e., temperate-like) habitats. But only two *Calandrinia* species and none of the last three genera are endemic to tropical latitudes. The diversity of all four genera centers in temperate latitudes. *Calandrinia* extends to Tierra del Fuego, and *Montiopsis* to ca. 40S. *Lenzia*, to my knowledge, does not enter tropical latitudes, yet is classified as Neotropical. Thus, the classification of *Calandrinia*, *Montiopsis*, and *Lenzia* as Neotropical is misleading or incorrect.

Oddly enough, *Cistanthe* and *Philippiamra*, the only genera classified (effectively) as temperate, are the most tropically distributed of Chilean Montiaceae. At least 12 *Cistanthe* species occur at tropical latitudes (Flores Fuentes 2016 and personal data), four of which are are endemic to Peru. *Cistanthe* diversity concentrates in Chile's Atacama and Coquimbo regions, and *Philippiamra* does not occur south of 30S. Segregation of *Philippiamra*, *Calyptridium*, and *Thingia* from *Cistanthe* significantly affects generic-level analysis in Chile. *Philippiamra* is South American, not antitropical, while its antitropical disjunction with closely related *Calyptridium* and *Thingia* is not apparent at the generic level. Likewise not apparent is the Circum-Pacific distribution of Montiaceae as a whole. Ironically, the classical conception of *Calandrinia* s. l. would have been classified as Circum-Pacific. The family's actual Circum-Pacific distribution remains, but it is no longer evident at the generic level. It is ironic that Moreira Muñoz (2011) overlooked this Montiaceae distribution, since it is the one that best indulges his panbiogeographic inclinations.

The inadequacies, inconsistencies, and artifacts of Moreira Muñoz' (2011) chorological/panbiogeographic classification of Chilean Montiaceae extends to other taxa, as well. For example, *Cruckshankia* (excluding *Oreopolis*; Rubiaceae), *Schizopetalum* (Brassicaceae), and *Schizanthus* (Solanaceae) all are genera of northern Chile, and the last extends well into tropical latitudes. Yet Muñoz Moreira (2011) included them in the temperate element, while *Calandrinia* and *Montiopsis* were classified as tropical. *Salpichroa* (Solanaceae) was classified in the Wide Neotropical track, the same as *Calandrinia*. But in contrast to primarily Chilean taxa, at temperate latitudes, *Salpichroa* species occur primarily on the east side of the Andes, with two species crossing the Chilean border. In other words, the phytogeography of taxa classified in the same floristic element and panbiogeographic track is intersecting, not coincident.

Some Andean genera, unlike *Salpichroa*, are diverse in both temperate Chile and east of the Andes. Depending upon species distributions, Moreira Muñoz (2011) classified these in either his Wide Neotropical (e.g., *Tropaeolum*, *Drimys*) or Central Andes – Southeast Brazil track (e.g., *Alstroemeria*). The classification is misleading insofar as it implies Neotropical "origins" of the temperate Chilean taxa. For example, *Tropaeolum* includes two clades, one temperate Chilean, the other Central Andean and S Amazonian. Although congeneric, genetic divergence between the clades is comparable to that separating families (Hershkovitz et al. 2006b). This suggests that *Tropaeolum* is not "Neotropical," but Gondwanan, the temperate Chilean and Neotropical Andean clades diversifying independently after the separation of South America. The same probably occurred in *Alstroemeria* and *Drimys* and perhaps other taxa.

Another peculiarity of Moreira Muñoz (2011) owes not to biogeographic epistemology, but to anthropocentrism. While it is axiomatic that a book on Chilean plant geography emphasizes plants occurring in Chile, Moreira Muñoz (2011) seems to treat geopolitical Chile as natural biogeographic entity. One senses that Chilean plant geography is consequent not so much to a half billion years of biological/geological evolution as it is to Chile's 1870s War of the Pacific and the Treaty of 1881, these respectively extending Chile's northern limit 8˚ in latitude and relinquishing Chile's claim to currently Argentinean Patagonia.

b. *Montiaceae in Chile versus the Chilean Floristic Region.* In contrast to Moreira Muñoz (2011), I use the term "Chilean" only as a global reference point, meaning "thereabouts." I use "Chilean flora" in an adjectival sense to refer to plants distributed/diversified primarily along the ca. 5000 X 150-200 km western slope of southwestern temperate to tropical South America. This includes the Argentinean Andes and southern coastal Peru. Native plant taxonomic representation here is biased, and, independent of taxonomic relations, the plants mostly have morphological/ecological characteristics especially adapted to the biotic/abiotic characteristics of the zone (Luebert & Weigend 2014).

Consequent to recent human political history, this biogeographic region largely coincides with continental geopolitical Chile. But geopolitical Chile intercalates with the biogeographically distinct altiplano in the north and Patagonian steppe in the extreme south. Hence it is convenient to refer to the characteristic (though composite) flora as "Chilean," even though it is not congruent geopolitically and does not include Easter Island. At one time, phytogeographic coincidence in this region with Chilean borders was less, and in pre-Columbian times, the phytogeography existed but Chile did not. At these times, the denomination "Chilean flora" would have been inadequate or inappropriate.

The term "Chilean floristic region" (ChFR, to not confuse with the CFR, the Cape Floristic Region) has been applied by Philip Rundel (pers. comm., 2019) to the phytogeographic region described above (INCOMME 2011). The ChFR is analogous to the California Floristic Province (CFP; Bunge et al 2016), which encompasses most of California and extends into adjacent

geopolitical territories. Also, the CFP, like the ChFR, is a composite flora, both ecologically and historically. Both include comparable desert, Mediterranean, and temperate forest elements having distinct spatiotemporal and phylogenetic origins. And both are influenced by similar climatic phenomena.

ChFR floristic composition (like that of geopolitical Chile) diverges more markedly latitudinally than CFP. This is why, historically, Chile's latitudinal floristic belts have been classified into different provinces (Moreira Muñoz 2011). The CFP is, or at least seems, more integrated latitudinally, especially because numerous dominant woody taxa span most or all of its length. Also, the CFP is ca. 50% more diverse than the ChFR, which itself offers more opportunity for latitudinal intergradation and integration. Large woody taxa in Chile have fewer species and they largely disappear from the landscape north of 30S. *Schinus* (Anacardiaceae) is an exception. And, of course, diversity approaches zero towards the maximally hyperarid zone. Nevertheless, the recognizable integrity of the ChFR is maintained, because many taxa span more than 20˚ latitude and two or more recognized floristic zones. Numerous genera present in fog oases at ca. 24S extend to at least central and some to austral ChFR zones (e.g., *Alstroemeria*, *Tropaeolum* sect. *Chilensis*). Meanwhile, more numerous taxa of central Chile extend to austral Chile, while others extend to the desert north. And this is aside from the many genera that are primarily Chilean but cross into the Argentinean Andes.

The ChFR's distinctive flora owes to several historical and modern biotic and abiotic contingencies (Moreira Muñoz 2011; Luebert & Weigend 2014). In modern times, the distinctiveness is corralled by three physical barriers, the Pacific Ocean (obviously), a very high and, just as importantly, steep mountain range, and the "arid diagonal," which extends from Chile's Antofagasta Region southeastward, cutting across Argentina's San Juan Province, towards Patagonia. North/northeast of the diagonal, a tropically-influenced macroclimate allows more Neotropical lineages to enter and intermix with ChFR taxa. But for most of Chile's length, the temperate Pacific macroclimate, aided by strong westerlies, facilitates entry of ChFR lineages into Argentinean territory, but mostly not beyond the High Andes. The consequence of the macroclimatic influence is that much of the southern cone flora endemic to the ChFR is not endemic to Chile. This applies to a majority of nonendemic native Chilean species and perhaps a third of the flora as a whole.

Moreira Muñoz (2011) did not afford a term for the ChFR; only the Flora of Chile and the various supra-Chilean and infra-Chilean regional floristic zones that historically have been described. He applied the term "subendemic," two times in reference to families having the ChFR distribution, but also in reference to Berberidopsidaceae, which has one Chilean and one Australasian genus. Thus, the term is not specific to the ChFR. He referred to one of 878 native genera as "subendemic," but no species. A large proportion of the genera classified in one or another of his nonendemic floristic elements, especially the Temperate element, pertain to the ChFR. In the chorological/ panbiogeographic classification, these ChFR genera are lumped with genera not pertaining to the ChFR.

Meanwhile, Moreira Muñoz' "endemic" criterion refers to genera contained within geopolitical Chile, including non-ChFR Easter Island, but not straying a micron into Argentina, Bolivia, or Peru. Even within continental Chile, this endemic "element" includes a biogeographically heterogeneous mix of taxa, some separated by 2000 or more km. No sense of geographical or phylogenetic relations of these genera was offered, not within Chile nor externally. It is as though the taxa evolved autonomously in an historically omnipresent Chile. Yet, the composition of the endemic, and, in fact, all of the elements would have differed according to prior territorial maps. The endemic element would gain taxa in the south and lose them in the north. Numerous taxa would lose Chile-Argentina distributions, while others would gain Chile-Bolivia(-Peru) distributions. Eventual cession of Chile-occupied Bolivia, Peru, and Wall Mapu would reduce Chilean plant generic endemism to close to zero.

Phylogeography of Montiaceae and probably most taxa distorts/disappears in the chorological/panbiogeographic analysis of Muñoz Moreira (2011). The preceding digressions demonstrate how epistemology and Umwelt influence biogeographic interpretation of taxa in general. Classical chorological analysis at arbitrary taxonomic levels might have – or at least have *had* – heuristic value. But as a means to an end, the approach is archaic and arcane. Processes that create chorological patterns are offset by processes that superimpose, intercalate, and erase them. The only way that the collective species of nearly 900 plant genera can be fit neatly into seven floristic elements and/or ten panbiogeographic tracks is with cut-and-paste or a bulldozer.

Meanwhile, the taxon-specific narrative analysis of Montiaceae yielded four major results. One is not only a phylogeographic description, but a hypothesis explaining the predominantly Circum-Pacific distribution of the family. Another is a description and explanation of the concentration of Montiaceae in Chile. In particular, Montiaceae help diagnose the ChFR. Of six Montiaceae genera in Chile, three are endemic not to Chile, but to the ChFR (*Lenzia*, *Montiopsis*, *Philippiamra*) and a fourth is essentially so, ignoring a pair of sister species in N America (*Cistanthe*). Twelve of 19 *Calandrinia* species are ChFR endemics and probably also the *Calandrinia* ancestor (see above). Yet, at most, only 2/19 species are endemic to geopolitical Chile (cf. Peralta & Ford-Werntz 2008, Elvebakk et al. 2015; see also below). Only the single species of *Montia* in Chile is truly allochthonous. Another conclusion is that Circum-Pacific Montiaceae (i.e., excluding *Phemeranthus*) originated in what is present day Chile (and/or what was not so long ago Bolivia and Peru). Finally, it revealed that Montiaceae evidently comprise the most globally successful plant lineage of ChFR origin.

The chorological/panbiogeographic approach to Chilean phytogeography (Moreira Muñoz 2011) failed to detect these phenomena. This owes to several factors. One is analysis at the taxonomic generic level, which "disappeared" the relations to excluded Australasian and North American Montiaceae. Assumption of generic monophyly is violated in the analyzed *Cistanthe* circumscription (as well as certain genera of other families). At the same time, it is understandable that the scope of the Chilean chorological tabulation logistically challenged analysis of 878 phylogenies. The chorological/panbiogeographic analysis itself was agnostic towards phylogeny, hence towards phylogeographic sources and sinks, hence the role of Chilean territory in Montiaceae diversification. This is not so much oversight as consequent to panbiogeographic epistemology, which focuses not on phylogeography, but on discovery of supposedly formerly continuous ranges. Finally, not consequent to chorology/panbiogeography per se, Moreira Muñoz' (2011) analyzed not a floristic region, but a geopolitical one, rendering an impression that recent geopolitical processes retroactively determine ancient biogeographic patterns.

c. *Vicariance and LDD – again.* The present work emphasizes the role of LDD in explaining Montiaceae distributions. The evidence will not convince those inclined to favor vicariance explanations. Moreira Muñoz (2011) provided a thorough and thoughtful review of the historical debate on the role of vicariance and LDD in explaining modern plant disjunct distributions, including epistemological aspects. There would seem little to add, but a few critical references were overlooked, additional evidence favoring LDD has emerged, and nonlinear evolutionary models offer additional insights.

The principal arguments of the vicariance/panbiogeographic school (e.g., Humphries & Parenti 1986, 1999; Heads 2009, 2014) and its apologists (e.g., Moreira Muñoz 2011) are that the appeal to LDD is ad hoc, it does not explain shared disjunction patterns globally parsimoniously, and, in any case, events resulting in LDD are rare. Implicit is that vicariance events are adequately frequent to explain the majority of disjunctions. Dispersalism dominated phytogeography until the latter 20th century. Then, abruptly, vicariance/panbiogeographic ideology became embedded dogma. Then a deluge of molecular evidence (including Hershkovitz & Zimmer 1997, 2000 for

Portulacineae) began to swing the pendulum the other way, suggesting a frequent role for LDD (Moreira Muñoz 2011). Yet, LDD had become so disparaged that even a decade later, evidence for LDD in a migratory *bird-dispersed* taxon was considered noteworthy/newsworthy (Donoghue 2011), perhaps on a par with the proof of cold fusion.

Much earlier, Hershkovitz & Zimmer (2000) argued that evidence for LDD was sufficiently pervasive to afford it a substantial *prior* likelihood to explain disjunctions in taxa that, like most Portulacineae, lacked LDD adaptations. This viewpoint evidently was novel and overlooked. It was not until Rees et al. (2005) that methods were developed that afforded a *post-analytical* likelihood to LDD. Lack of LDD adaptation remained a principal stumbling block in acceptance of LDD explanation, e.g., Moreira Muñoz (2011: *120*).

Subsequent theoretical and empirical evidence confirmed the notion of Hershkovitz & Zimmer (2000). Nathan (2006; Nathan et al. 2008) demonstrated that the cumulative probability density functions of LDD frequency and distance for non-LDD-adapted propagules are fat-tailed. In other words, given enough time, LDD is bound to occur. The actual probability is a function of "nonstandard" vector frequency, e.g., hurricanes, tsunamis, or nonstandard zoophily. A nonstandard vector is any vector that is not the one or among those that normally disperse the overwhelming majority of propagules. Thus, lack of LDD adaptation is a red herring in phylogeographic debate.

But nonstandard vectoring is much more frequent than vicariance/panbiogeographic adherents would suggest. A single successful hurricane/tsunami-facilitated LDD per century for 10 million years yields 100,000 LDDs, presumably far more than the number of plant phylogenetic long-distance disjunctions. Yet, the number of strong hurricane/tsunami events is much greater than one per century, and each is capable of facilitating multiple LDDs. The negative correlation between frequency/force of catastrophic events is offset by the positive correlation between event force and number/distance of propagules dispersed. Adding birds to the equation, a single bird-facilitated LDD per year would yield 10 million LDDs, overshadowing catastrophic LDD frequency. But the number of long distance bird migrations annually likely is >10 billion (Viana et al. 2016; Dokter et al. 2018), yielding 10^{17} LDD opportunities over 10 million years.

The evidence suggests that the supposition of infrequency of LDD vectoring opportunities is, at least, "incompetent, irrelevant, and immaterial," and, at most, patently false and absurd. If anything, the number of observed disjunctions among Montiaceae and Portulacineae generally is not higher, but *lower* than expected via LDD. In the case of Montiaceae, assuming a 50 million year age, it amounts to less than one successful dispersal every two million years. Of course, most observed disjunctions are at the interspecific level (i.e., recent), so the rate obviously must be much higher. In other words, the 50 million year calculation ignores lineage extinction. At the same time, the more recent the disjunction, the less likely it owes to vicariance. But as Nathan (2006; Nathan et al. 2008) notes, the factor limiting successful LDD is not dispersal itself, but the low likelihood of establishment of the propagule.

Upchurch (2008) agued that, because of unseen events such as range expansion, vicariance/dispersal analysis will tend to bias in favor of dispersal. He is correct that unseen events can distort interpretation of historical relations. Correcting for unseen events is the point of probabilistic parametric models in likelihood analysis. However, Upchurch (2008) did not appreciate that bias is a double-edged sword. For example, the evidently recent spread of *Montia* into South America may render more plausible the notion that the Australasian disjunction is vicariant, since these areas were connected in the Cretaceous and separate from Laurasia since the Triassic.

However, a more important overlooked bias is that loss of vicariance approximates Dollo's Law, while loss of LDD disjunction does not. More precisely, a vicariant relationship can occur only

once, when connected areas are separated. This relationship is broken when either descendent lineage becomes extinct – which is inevitable. Thereafter, areas rarely become reconnected, e.g., India, Panama, Beringia, but usually long after biota on both sides have evolved substantially. However, reconnection/reseparation of land areas does not recreate vicariance. Ontologically, vicariance relations cannot reestablish

Alternatively, the LDD clock begins ticking immediately after separation. Its probability is highest the soonest after area separation, but the "fat tail" of the LDD probability density function maintains its likelihood thereafter. And possibly the former presence of a taxon in a separated terrain renders more likely the success of related taxa dispersed to that terrain (Thuiller et al. 2010). LDD thus can create "pseudovicariance," or cases where vicariance appears or is actually plausible, yet did not occur. In addition, LDD can distort apparent vicariance relations if there is gene flow between vicariant and subsequently dispersed individuals.

Additional criticisms of molecular phylogenetic and molecular clock-based LDD conclusions include the possibility of lineage sorting and unreliability of molecular dating methods (Heads 2009, 2014). Evidence discussed earlier in this work makes clear that these concerns are valid. But, in the present context, they also are red herrings, because they can bias data in both directions. Moreover, an argument for greater lineage antiquity does not necessarily favor vicariance, because, as noted, the older the lineage, the more likely that it has experienced LDD.

Dismissal of fossil absence as "negative evidence" also is unjustified. Heads (2014) especially attributes broad disjunctions of locally restricted modern species to former widespread ranges, ignoring absence of corresponding fossils. Indeed, vicariance seems to require broad taxon ranges, as taxa with smaller ranges and more locally restricted populations are less likely to span rift zones, and rift zones themselves are not conducive to survival of normally inland species. However, the broader the range and more frequent the taxon, the more likely is its fossil preservation. And the older the lineage, the less likely that its fossil preservation will be delayed tens of millions of years. Thus, the present interpretation of a mainly or completely LDD-mediated Montiaceae distribution is only partly based on phylogenetic and molecular dating evidence. It is based on the logic that the absence of Paleocene/Eocene fossils, if not positive evidence that Portulacineae, including Montiaceae, were absent, is at least positive evidence that the lineage was not broadly distributed across Gondwana.

Thus, the panbiogeographic/vicariance idealization distributed worldwide during the late 20th century evidently persists relictually mainly in isolated Gondwanan fragments (e.g., Upchurch 2008; Heads 2009, 2014; Moreira Muñoz 2011). Vicariant disjunctions certainly exist, but Hershkovitz and Zimmer's (2000) then-blasphemous proposal that LDD merits a high prior likelihood now seems modest. In the case of plant disjunctions, LDD not only should be afforded a prior likelihood, it qualifies as the default assumption. It is vicariance that demands positive evidence in the form of contemporaneous fossils, and in not one, but *both* of the formerly connected areas.

d. *Closing remarks: biology, geology, and biogeography*. Moreira Muñoz' (2011) defense and application of chorology/panbiogeography roots in his argument that biogeography is an independent discipline. Biogeographers draw on phenomenologically independent biological and geological events, and, like their astrological brethren, align them, discern patterns, and make predictions. Historically, this approach has "worked" only once, predicting the principle of plate tectonics. A half century ago, chorology, especially in zoology, figured significantly in corroborating plate tectonic theory (e.g., P. Hershkovitz 1969, 1972). But even by then, the utility of panbiogeographic research was questioned (e.g., P. Hershkovitz 1972: *331*), its resonance with plate tectonic theory notwithstanding. And notwithstanding its role in advancing plate tectonic theory,

chorology has not yielded since a new, comparably significant discovery. Rather, its role has been limited, and to questionable effect, to the hashing out of consequent biogeographic details.

In theory, biogeography should privilege neither biological nor geological dogma. In practice, this is not always so. Panbiogeographers seem to afford greater predictive power to geology. But in systematics, biology has been privileged. As Moreira Muñoz (2011) and others have noted, most phytogeographic research is undertaken not by card-carrying geographers, but by systematists (i.e., biologists), often as a convenient pretext for justifying mass DNA sequencing projects. The objective generally is to explain the geographical history of particular organisms, not the geographical history of land areas.

Moreira Muñoz' (2011) points are well-taken here, yet I maintain that biological evidence must be privileged in biogeography. Certainly, as demonstrated here, taxonomy and taxonomic relations presumed in biogeographical analysis are theory-laden. The same applies to a priori presumed geographic areas. But the privilege of biology owes to a different factor altogether. Specifically, while geology and biogeographic patterning indeed provide critical and independent data for explaining/predicting particular plant distributions, geology and geographic patterns absolutely *never* have *determined* the distribution of any biological organism. They merely provide boundary conditions. Distributions are determined by the enactivity of the organisms themselves (Hershkovitz 2018c; cf. Maturana & Varela 1992; Varela et al. 1992; Maturana & Mpodozis 2000). Geographical survival and persistence of organisms is not chiseled into (fragmented) stone. Stones cannot force their will on organisms. The "choice" (*not* in a teleological sense) to live and reproduce in a particular location is made by the organism and not the location itself, much less statistics or ideology.

But Hershkovitz (2018a, b) also emphasized the precariousness of evolutionary reconstruction, hence the limitation biology consequently imposes on phylogeographic analysis. However complex is historical geological reconstruction, its processes seem to conform to linear stochastic physical models. Organismal evolution, in contrast, is a nonlinear idiosyncratic process (Hershkovitz 2018c). Modern patterns of Montiaceae phylogeographic distribution developed over the course of tens of millions of years of their biological evolution. Many biologically plausible evolutionary scenarios could generate their present forms and distributions, and no plausible scenario can be falsified unequivocally. Moreover, modern Montiaceae species diversification evidently transpired mainly during the Pliocene and continued up until the Pleistocene. The absence of fossils renders difficult the reconstruction of the morphology and ecology of Montiaceae ancestors between the time of their late Eocene (or earlier) origins and the Miocene/Pliocene. Yet, this unrecoverable history is critical to phylogeographic reconstruction. In phylogenetics, the very existence of these real but disembodied ancestors is reduced to a few sterile, abstract lines on a phylogram. Possibly the complexity of tens of millions of years of biological and terrestrial evolution is so mind-boggling that the mind short-circuits and reduces it conceptually to an instant and attempts to explain it correspondingly simplistically.

6. Synopsis of Subfamilial and Generic Taxonomy of Montiaceae

This work concludes with a summary of a subfamilial to subgeneric level taxonomy of Montiaceae, modified from Hernández-Ledesma et al. (2015) according to current phylogenetic evidence (see above). Each taxon comprises a clade. Numbers/letters in bold denote cladistic rank. Vertically aligned taxon names share cladistic rank. Rank suffixes, when applied, accord with conventional classification (McNeill et al. 2011). But, above the generic level, no conventional nomenclatural ranks are assigned per Cantino and De Queiroz (2007). Thus, missing conventional nomenclatural ranks can be assigned if so desired.

MONTIACEAE Raf.

1. MONTIOIDEAE
1A. MONTIEAE
1A1. MONTIINAE
1A1a. *Montia* L.
1A1b. *Claytonia* L.
1A2. *Lewisia* Pursh
1A3. *Lewisiopsis* Govaerts
1B. *Calandrinia* Kunth
1C. **HECTORELLEAE** Appleq., Nepokr. & W.L. Wagner
1C1. *Hectorella* Hook. f.
1C2. *Lyallia* Hook. f.
2. *Rumicastrum* Ulbrich
3. **CISTANTHEAE** Hershk.
3A. *Cistanthe* Spach
3B. *Montiopsis* Kuntze
3C. **CALYPTRIDINAE** Hershk.
3C1. *Calyptridium* Nutt. in Torr. & A. Gray
3C2. *Thingia* Hershk.
3C3. *Philippiamra* Kuntze
3C4. *Lenzia* Phil.
4. **PHEMERANTHEAE** Hershk.
4A. *Phemeranthus* Raf.
4B. *Schreiteria* Carolin

The taxonomy below elaborates the synopsis above to the subgeneric level and includes estimated species numbers, distributions, and relevant clarifications and commentary. Conventional ranks are retained at the subgeneric level, because these have somewhat greater application in practice than suprageneric taxa. Monophyly of species is not presumed nor generally in evidence.

MONTIACEAE Raf.

1. MONTIOIDEAE

1A. MONTIEAE

1A1. MONTIINAE

Historically, the generic taxonomy in this clade has been unstable and somewhat confusing, such that most species have homotypic synonyms in multiple genera (O'Quinn et al. 2005), and many in both *Claytonia* and *Montia*. Because taxonomic references are not self-correcting, the problem persists, e.g., in Marinho et al. (2019).

1A1a. MONTIA L., Sp. Pl. 1: 87. 1753. **TYPE**: *Montia fontana* L.

Claytonia sect. *Alsinastrum* Torr. & A. Gray, Fl. N. Amer. 1(2): 201. 1838.

Claytonia sect. *Naiocrene* Torr. & A. Gray, Fl. N. Amer. 1(2): 201. 1838.

Claytonia subsect. *Montiastrum* A. Gray, Proc. Amer. Acad. Arts 22: 283. 1887.

Crunocallis Rydb., Bull. Torrey Bot. Club 33: 139. 1906.

Naiocrene (Torr. & A. Gray) Rydb., Bull. Torrey Bot. Club 33: 139. 1906.

Montiastrum (A. Gray) Rydb., Fl. Rocky Mts. 265. 1917.

Claytonia sect. *Australiensis* Poelln., Repert. Spec. Nov. Regni Veg. 30. 1932.

Limnalsine Rydb., N. Amer. Fl. 21 (4): 25. 1932.

Mona Ö. Nillson, Bot. Not. 119: 266. 1966.

Neopaxia Ö. Nilsson, Bot. Not. 119: 469. 1966.

Maxia Ö. Nillson, Grana Palynol. 7: 359. 1967.

Claytoniella Jurtzev, Bot. Zhurn. (Moscow & Leningrad) 57: 644. 1972.

Ca. 19 annual and perennial (rooting at nodes) species; eight in W North America to NE Asia, one in N South America, seven in New Zealand, one in Australia, and one cosmopolitan (O'Quinn et al. 2005; Heenon 2007). How much of the range of the cosmopolitan *Montia fontana* is natural versus anthropogenic is not clear. Polymorphic, more than 30 heterotypic taxa are included in its synonymy (Tropicos.org 2018). Within the past 50 years, *Montia linearis* (Dougl. ex Hook.) Greene has expanded to lower elevations adjacent to its past native range and has become adventive in the central and eastern US and in Europe (Hershkovitz 1998a; Dembicz et al. 2015). *Montia parvifolia* is reportedly adventive in the UK (GBIF Secretariat 2017). *Montia chamissoi* is distributed mainly in W North America, but it has established more recently in midwestern and eastern US states (GBIF Secretariat 2017). Whether or not these occurrences are natural or anthropogenic is not clear. This species also is widely disjunct in S Mexico (GBIF Secretariat 2017).

O'Quinn et al. (2005) recognized three monophyletic sections based on molecular phylogenetic evidence. No attempt will be made here to list all of the synonyms implicated. The sections distinguish in pollen morphology.

1A1a1. M. sect. **MONTIA**

Ca. six species evidently originally of W North America, including the widespread *M. fontana*, and the apparently adventive *M. chamissoi* and *M. parviflora*. The species share pollen aperture membranes bearing a single row of projections.

1A1a2. M. sect. **AUSTRALIENSIS** (Poelln.) Pax & K. Hoffm., Die Natürlichen Pflanzenfamilien, ed. 2, 16c: 282. 1934. *Claytonia* sect. *Australiensis* Poelln., *Paxia* Ö. Nilss., *Neopaxia* Ö. Nilsson. **TYPE:** *Montia australasica* (Hook. f.) Pax & K. Hoffm. Synonyms: *Claytonia australasica* Hook. f. *Neopaxia australasica* (Hook. f.) Ö. Nilsson. *Paxia australasica* (Hook. f.) Ö. Nilsson.

Nine species, eight in Australia/New Zealand and one in NW North America and SW Canada. The species share pollen aperture membranes with 2–3 rows of projections.

1A1a3. M. sect. **MONTIASTRUM** (A. Gray) Pax & K. Hoffm. Die Natürlichen Pflanzenfamilien, ed. 2, 16c: 259. 1934. *Claytonia* sect. *Montiastrum* A. Gray. *Montiastrum* (A. Gray) Rydb. **TYPE:** *Montia linearis* (Douglas ex Hook.) Greene. Synonyms: *Claytonia linearis* Douglas ex Hook., *Montiastrum lineare* (Douglas ex Hook.) Rydb.

Four species of NW North America and NE Asia, including the adventive *M. linearis*. The species share tholate pollen aperture membranes.

1A1b. CLAYTONIA L., Sp. Pl. 1: 204. 1753. *Claytonia* [unranked] *Euclaytonia* Walp., Repert. Bot. Syst. 2: 237. 1843 (*nom. inval.*). *Claytonia* [unranked] *Cormosae* A. Gray, Proc. Amer. Acad. Arts 22: 278. 1887. *Claytonia* sect. *Cormosae* A. Gray ex Poelln., Repert. Spec. Nov. **TYPE**: *Claytonia virginica* L.

Belia Steller ex S.G. Gmel., Fl. Sibir. 4: 88. 1769.

Limnia Haw., Syn. Pl. Succ. 11. 1812. *Claytonia* sect. *Limnia* (Haw.) Torr. & A. Gray, Fl. N. Amer. 1: 199. 1838. *Montia* sect. *Limnia* (Haw.) B.L. Rob., Syn. Fl. N. Amer. 1: 273. 1897. *Claytonia* subg. *Limnia* (Haw.) Holub, Preslia 47: 328. 1975.

Claytonia [unranked] *Caudicosae* A. Gray, Proc. Amer. Acad. Arts 22: 279. 1887.

Claytonia [unranked] *Rhizomatosae* A. Gray, Proc. Amer. Acad. Arts 22: 280. 1887. *Montia* [unranked] *Rhizomatosae* (A. Gray) B.L. Rob., Syn. Fl. N. Amer. 1: 272. 1897. *Claytonia* sect. *Rhizomatosae* (A. Gray) Poelln., Repert. Spec. Nov. Regni Veg. 30: 281, 296. 1932.

Claytonia sect. *Chenopodinae* Poelln., Repert. Spec. Nov. Regni Veg. 30: 280. 1932.

Ca. 33 species with ca. 20 additional recognized subspecific taxa, mostly in W North America and NE Asia, two extending to S Mexico and one to N Guatemala (O'Quinn et al. 2005; Miller & Chambers 2006; Stoughton et al. 2017a, b). *Claytonia sibirica* and *C. perfoliata* are adventive in Europe, Australia, and New Zealand, and the latter also in Argentina (Howell & Sawyer 2006; Miller & Chambers 2006; GBIF Secretariat 2017; Atlas of Living Australia 2018).

With a minor exception, subgeneric cladistic classification of *Claytonia* (O'Quinn et al. 2005) corresponds approximately to the classical classification according to life form (annual, rhizomatous, tuberous, caudiciform), except that the last two form a single undifferentiated clade. None of the three principal life form clades is paraphyletic with respect to any other. O'Quinn et al. (2005) recognized three sections; again, no attempt is made here to elaborate the synonymy. Discrepancies persist in the number of taxa recognized (O'Quinn et al. 2005; Miller & Chambers 2006; Stoughton et al. 2017a, b). The genus is known for variability in karyotype and ploidy.

1A1b1. CLAYTONIA sect. **CLAYTONIA**

Ca. 16 species plus 12 additional subspecific taxa; tuberous or tap-rooted caudiciform perennials. Although the two growth forms are conspicuously distinct morphologically, their genetic

divergence is low, and evidently the tap-rooted form has evolved more than once or species having different growth forms have evolved reticulately (O'Quinn et al. 2005). Whole-genome DNA sequence sampling and analysis has revealed evidence of ancient hybridization and/or genetic lineage sorting among several species (Stoughton 2017a). Evidently, unclassifiable individuals are not uncommon. This section has the broadest climate niche of any Montiaceae taxon, ranging from Siberia southwards along the cordillera to Mexico and then eastward to Atlantic and Gulf of Mexico states, and with a MAP gradient spanning ca. 5–5000 mm.

1A1b2. CLAYTONIA sect. **LIMNIA** (Haw.) Torr. & A. Gray, Fl. N. Amer. 1: 199. 1838. *Limnia* Haw., *Montia* sect. *Limnia* (Haw.) B.L. Rob. *Claytonia* subg. *Limnia* (Haw.) Holub. **TYPE:** *Claytonia sibirica* L. Synonyms: *Limnia sibirica* (L.) Haw. *Montia sibirica* (L.) Howell.

Ca. nine species plus eight additional subspecific taxa; annuals and two facultatively stoloniferous perennials. One species may behave as a winter annual (Miller & Chambers 2006; Hershkovitz 2017b). Reportedly, subspecific taxa of both the *Claytonia perfoliata* and *C. rubra* complexes intergrade, as do the two species complexes with each other (Miller & Chambers 2006, 2012b). Hybridization is suspected, but lineage sorting also emerges as a cause, especially given the frequency of polyploidy (cf. McIntyre 2012).

1A1b2. CLAYTONIA sect. **RHIZOMATOSAE** A. Gray ex Poelln., Repert. Spec. Nov. Regni Veg. 30: 281, 296. 1932. *Claytonia* [unranked] *Rhizomatosae* A. Gray., *Montia* [unranked] *Rhizomatosae* (A. Gray) B.L. Rob. in A. Gray & S. Watson. **TYPE:** *Claytonia sarmentosa* C.A. Meyer. Synonyms: *Montia sarmentosa* (C.A. Meyer) B.L. Rob. in A. Gray & S. Watson. *Limnia sarmentosa* (C.A. Meyer) Rydb.

Eight species, one annual and seven rhizomatous perennials. The perennials evidently are monophyletic (O'Quinn et al. 2005).

1A2. LEWISIA Pursh, Fl. Amer. Sept. 2: 360. 1813. **TYPE**: *Lewisia rediviva* Pursh.

Erocallis Rydberg, Bull. Torrey Bot. Club 33: 139. 1906.

Oreobroma Howell, Erythea 1: 31. 1893.

Ca. 18 perennial species plus six additional subspecific taxa of W North America, concentrated in California, extending into S Canada and NW Mexico (Hershkovitz & Hogan 2002; Wilson et al. 2005).

Limited molecular/phylogenomic data (Goolsby et al. 2018a, b; Hershkovitz, unpublished) evidence two major clades, one comprising *Lewisia* sect. *Cotyledon* excluding *L. congdonii*. The latter resembles species of this section morphologically, but its leaves are ephemeral like those of the remainder of the genus. The remaining species variously classified into several sections (Mathew 1989; Davidson 2000) also form a clade, but their interrelations remain unresolved and possibly are irresolvable cladistically. Thus, the genus is classified here into two subtaxa.

1A2a. LEWISIA sect. **LEWISIA**

At least 13 (likely more) perennial species plus one commonly accepted subspecific taxon (Hershkovitz & Hogan 2002; Wilson et al. 2005) of W North America, concentrated in California, extending into S Canada and NW Mexico. Taxonomy of the species varies markedly in various treatments, and no attempt is made here to resolve it definitively. Limited molecular/phylogenomic data (Goolsby et al. 2018a, b; Hershkovitz, unpublished) show no correspondence to any proposed sectional taxonomy of the included species. The data confirm the suspected historical complexity of plants conservatively classified as *L. pygmaea* by Hershkovitz & Hogan (2002). The species complex evidently is polyphyletic, but the limited data do not adequately investigate the degree of reticulate evolution likely in this genus, whose species manifest a considerable degree of interfertility (Mathew 1989; Davidson 2000). Available molecular/phylogenomic data indicate that *L. congdonii* is well-nested within this section. Its morphology hints that it may have an intersectional hybrid origin. Perennating structures of this section span the range observed in *Claytonia* sect. *Claytonia*, viz., ranging from deep, sinuous to shorter fusiform taproots to globose tubers.

1A2b. LEWISIA sect. **COTYLEDON** J.E. Hohn ex B. Mathew, The Genus *Lewisia*: 139. **LECTOTYPE** (designated here): *L. cotyledon* (S. Watson) B.L. Rob. in A. Gray. Synonyms: *Calandrinia cotyledon* S. Watson. *Oreobroma cotyledon* (S. Watson) J.T. Howell.

Excluding *L. congdonii*, this section comprises three allopatric species complexes and their variably recognized segregates/subtaxa, plus one interspecific hybrid taxon as follows: **(i)** *Lewisia cantelovii* J.T. Howell (incl. 2–3 subtaxa) of the east slope of the Sacramento River drainage in California; **(ii)** *L. cotyledon* (incl. 3–4 subtaxa) of the Klamath region in NW California, **(iii)** *L. columbiana* (Howell ex A. Gray) B.L. Rob. in A. Gray (incl. 3 subtaxa) of the Pacific NW US and SW British Columbia; and **(iv)** *L. leeana* (Porter) B.L. Rob. in A. Gray of the Klamath region, with an outlying population in central California. The last is believed to be a hybrid between *L. columbiana* and *L. cotyledon*. Subtaxa of the *L. cotyledon* complex are sympatric/parapatric and intergrading. Those of the other two complexes are distinct geographically and morphologically, hence species designation is defensible. Their subspecific status owes to their geographic restriction, rarity, and taxonomic inertia. In terms of biodiversity accounting, regardless of taxonomic preference, I prefer to think of *L.* sect. *Cotyledon* as comprising eight species plus two additional subspecific taxa (two of the three *L. cotyledon* subtaxa).

1A3. LEWISIOPSIS Govaerts, World Checkl. Seed Pl. 3(1): 21. 1999. *Lewisia* subg. *Strophiolum* J.E. Hohn ex B. Mathew, The Genus *Lewisia* 139. 1989. *Cistanthe* sect. *Strophiolum* (J.E. Hohn ex B. Mathew) Hershk., Phytologia 68: 268. 1990. **TYPE**: *L. tweedyi* (A. Gray) Govaerts. Synonyms: *Calandrinia tweedyi* A. Gray. *Lewisia tweedyi* (A. Gray) B.L. Rob. in A. Gray. *Cistanthe tweedyi* (A. Gray) Hershk.

One perennial species of central Washington State, USA, extending into southernmost British Columbia, Canada (Mathew 1989; Davidson 2000).

On morphological evidence, Hershkovitz (1990a, b, 1991a, 1992, 1993a) transferred this taxon from *Lewisia* (Mathew 1989; Davidson 2000) to *Cistanthe*, later retreating from this position based on molecular evidence (Hershkovitz & Zimmer 1997, 2000; Hershkovitz 2006). Hershkovitz (2018a) cites molecular evidence that *Lewisiopsis* originated as a hybrid between early divergent ancestors of *Lewisia* and Montiinae, followed by polyploidization and sequestering of further evolutionary change. This, in turn, explains phenotypic similarities between *Lewisiopsis* and *Cistanthe*.

1B. CALANDRINIA Kunth (*nom. cons.*), Humb., Bonpl. & Kunth, Nov. Gen. Pl. (fol. ed.) 6: 62. 1823. **TYPE**: *C. ciliata* (Ruiz & Pav.) DC. (*nom. cons.*). Synonym: *Talinum ciliatum* Ruiz & Pav.

Cosmia Dombey ex Juss., Gen. Pl. 312. 1789., *obs.*

Baitaria Ruiz & Pav., Fl. Peruv. Prodr. 63. 1794.

Tutuca Molina, Sag. Stor. Nat. Chile, ed. 2. 135. 1810.

Geunsia Moc. & Sessé ex DC, Prodr. 3: 358. 1828, *nom. inval.*

Phacosperma Haw., Philos. Mag. Ann. Chem. 2 (1): 123. 1827.

Monocosmia Fenzl, Nov. Stirp. Dec. 84. 1839.

? *Diazia* Phil., Fl. Atacam. 22. 1860.

Ca. 17 annual and perennial herbaceous species of W North America and W South America (Hershkovitz 2006; Peralta & Ford-Werntz 2008; Elvebakk et al. 2015).

The genus *Tutuca* Molina is recognized here as a synonym of *Calandrinia* based on its original characterization and illustration in Feuillée (1725). The sole species, *T. chilensis* Molina, likely is *C. compressa* Schrad. ex DC. A subsequently published name, *T. fistulosa* Molina, evidently refers to this same type and is superfluous (cf. Gunckel 1972). Hooker and Arnott (1833,1841 [1830]) included "*Tutuca* Feuillée" in synonymy with (effectively) *Calandrinia compressa*, and Philippi (1867) shared this opinion. Gunckel (1972) (mis-)identified *Tutuca chilensis/fistulosa* as *Senecio fistulosa* (Molina) Poeppig ex Lessing. The International Plant Names Index (2012) erroneously refers *Tutuca* to Ericaceae.

Hershkovitz (2018a) classified *Diazia* as incertae sedis. Since that work was posted, I obtained and examined an image of the supposed type specimen, *Diaz 87* (SGO!), and found that I had annotated it in 1992 as *Calandrinia ciliata* (Ruiz and Pav.) DC. Indeed the specimen itself pertains to *Calandrinia*, but the identity of the specimen with the type of *Diazia* was questioned in a prior annotation by Rebecca Acevedo. Carolin (1993) included *Diazia* in *Philippiamra* as circumscribed below.

The current cladistic circumscription of *Calandrinia* was proposed in Hershkovitz (1990b), based on intuitive interpretation of morphology. The circumscription differed from the previous (and first) cladistic circumscription (Carolin 1987, 1993), which classified the annual species in this genus, but classified the perennial species in *Baitaria*, along with all species of *Montiopsis*. Monophyly of the current circumscription has been confirmed by all six subsequent molecular analyses cited in this work, including Hancock et al. (2018), who proposed a different circumscription (see below).

Calandrinia s. l. is an example of a classical so-called "evolutionary" taxon. These were conceptually fundamentally Aristotelian (Scala Natural) in that taxa were conceived hierarchically according to their perceived degree of evolutionary specialization. "Higher" or "advanced" taxa emerged from "lower" or "primitive" taxa (e.g., "lower vascular plants"), the latter cladistically paraphyletic. Segregation of perceptually specialized advanced taxa left taxonomic receptacles to which were relegated more perceptually primitive taxa. *Calandrinia* s. l. was such a receptacle. It was not, nor intended to embody, a monophyletic taxon. It was the receptacle for largely western American and Australian species with most or all of the following traits: hemicryptophytic herbs,

hypogynous flowers, conspicuous corolla of five petals, five-plus stamens, three carpels, and a basipetally dehiscent valvate capsule with many seeds. Otherwise, the species were morphologically heterogeneous and classified into 12 American and six Australian sections (Carolin 1987, 1993). The traits delimiting *Calandrinia* s. l. were not good indicators of relationship. For example, achenial species segregated into other genera and even classified in different classical tribes (McNeill 1974) proved to be otherwise morphologically and genetically very closely related to certain *Calandrinia* s. l. species (Hershkovitz 1993a, 2000, 2006).

Apparent taxonomic confusion following the cladistic dissection of *Calandrinia* s. l. owes to several factors. One was the historical fact that, at the time, much, if not most, of the plant taxonomic community did not embrace or yet understand the emerging paradigm of cladistics and/or the logic of cladistic taxonomy. Many subsequent research and reference works continued to apply the classical classification.

Another factor was the failure to appreciate that the cladistic realignments divided *Calandrinia* s. l. along existing taxonomic lines. While the sectional taxonomy per se was not cladistic, cladistic partitions coincided with groups of sections. The morphological distinctions between these groups of sections are unambiguous. In fact, the distinctions between these groupings are less ambiguous than the distinctions between *Calandrinia* s. l. and other classical genera. However, in scientific practice, taxonomy emphasizes only genus and species and not intervening ranks. Thus, non-specialists were unfamiliar with the sectional taxonomy, and the cladistic generic classification seemed arbitrary, if not incomprehensible.

Another factor was "taxonomic provincialism." Regional floristic taxonomists historically tended to perceive, hence classify, new taxa in a local rather than global context. Sometimes, workers simply were unfamiliar with global diversity of local genera. For example, a few species of South American and Australian Montiaceae described as *Calandrinia* s. l. proved to be species of *Phemeranthus*, *Talinum* (Talinaceae), or *Anacampseros* (Anacampserotaceae). But regional specialists classified them in the regionally predominant *Calandrinia* s. lato.

A final exacerbating factor may have been the long delay in transferring species to their new genera. Roger Carolin had prepared but never published catalogs of binomial recombinations according to his cladistic classification. These catalogs recombined *all* existing typified binomials, whether or not the corresponding species were taxonomically accepted. I believed that half or more of these recombinations effectively created new taxonomic synonyms. But as I was primarily a higher taxon specialist, I urged my species taxonomy specialist colleagues to assume the recombination effort. For reasons articulated above, the process was delayed for several years. For my part, I had recombined binomials only as necessary to refer to the corresponding (often misidentified) species in my phylogenetic work and, in Hershkovitz (2006), not even then. Consequently, the taxonomy, especially of *Cistanthe*, persisted in a chaotic state, a haphazard mixture of new and old binomials and misidentifications. Naturally, this did not aid in appreciation of the cladistic generic distinctions. In retrospect, Carolin's unilateral shotgun approach was the more prudent.

1B1. CALANDRINIA sect. CALANDRINIA

Calandrinia sect. *Compressae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Axillares* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Monocosmia* (Fenzl) Hershk., Phytologia 70: 223. 1991.

Ca. 8 annual species native to western America, distributed along the American cordillera nearly from British Colombia to SW USA and NW Mexico, central Mexico to the Central Andes of N Argentina (except Panama), Buenos Aires Province in Argentina, throughout all but the southernmost ChFR, and one species possibly native to the Falkland Islands (Hershkovitz 2006; Peralta & Ford-Werntz 2008). *Calandrinia menziesii* is adventive on other continents/islands (Hershkovitz 2006). Most recently it has been collected several times in central Louisiana (GBIF Secretariat 2017), but I am unable to determine whether it is established there. *Calandrinia compressa* has been collected in Europe (GBIF Secretariat 2017), but its establishment status reports are conflicting. Possibly the reports reflect transitory escapes from cultivation. The species is established, however, in New Zealand (Howell & Sawyer 2006). At least one undescribed species occurs in Patagonia, but revision of these taxa is not undertaken here.

Five molecular phylogenetic analyses (Hershkovitz & Zimmer 2000; Hershkovitz 2006; Ogburn & Edwards 2015) indicate that this section is monophyletic, but a more recent phylogenomic analysis (Goolsby 2018a, b) shows this section as paraphyletic with respect to the perennial clade, *C.* sect. *Caespitosae*, with the annual *C. nitida* (synonym: *C. axilliflora*) as sister to the latter. Hershkovitz (1993a) suggested the reverse relation, with the perennials paraphyletic to the annuals. Interestingly, however, *C. nitida* was cited as the morphologically transitional taxon.

1B2. CALANDRINIA sect. **CAESPITOSAE** Philippi, Anales Univ. Chile 85: 175. 1893. *Baitaria* Ruiz & Pav. l.c. **LECTOTYPE** (designated here): *C. acaulis* Kunth.

Calandrinia sect. *Acaules* Reiche, Ber. Deutsch. Bot. Ges. 15: 500. 1897.

Ca. 11 perennial species plus one variety of W South America, mostly of the ChFR, two species of the Central Andes, one extending to Central America and southern Mexico (Hershkovitz 2006; Peralta & Ford-Werntz 2008; Elvebakk et al. 2015).

Researchers (e.g., Carolin 1987, 1993; Hershkovitz 1991e, 1993a, etc.) have applied Reiche's sectional name *Acaules*, but Philippi's earlier name appears to be valid. All molecular/phylogenomic analyses cited in this work indicate that this section is monophyletic (see above). Taxonomy of the central Andean plants (Argentina, Bolivia, Chile, and Peru) remains problematic. Hershkovitz & Ford[-Werntz] (1993) renamed *Baitaria acaulis* Ruiz & Pav. as *Calandrinia carolinii* Hershk. & D.I. Ford. The type collection is mixed and includes individuals identified as *Calandrinia acaulis* Kunth. But Hershkovitz & Ford[-Werntz] (1993) did not resolve definitively the taxonomic identity of *C. carolinii*. Peralta & Ford-Werntz (2008) applied the name *C. carolinii* to plants distinct from *C. acaulis*.

1C. HECTORELLEAE Appleq., Nepokr. & W.L. Wagner, Syst. Bot. 31: 316. 2006. **TYPE:** *Hectorella* Hook. f.

1C1. HECTORELLA Hook. f., Handb. N. Zeal. Fl. 27.1864. **TYPE**: *Hectorella caespitosa* Hook. f. Synonym: *Lyallia caespitosa* (Hook. f.) Nyanyano & Heywood.

One perennial species of New Zealand (Applequist et al. 2006; Wagstaff & Hennion 2007).

1C2. LYALLIA Hook. f., Bot. Antarct. Voy. Antarct. (Fl. Antarct.) 2: 548, t. 122. 1847. **TYPE**: *Lyallia kerguelensis* Hook. f.

One perennial species of the Kerguelen Islands (Applequist et al. 2006; Wagstaff & Hennion 2007).

2. RUMICASTRUM Ulbrich, Engler & Prantl, Nat. Planzenfam. 16c: 519. 1934. **TYPE**: *Rumicastrum chamaecladum* (Diels) Ulbrich. Synonym: *Atriplex chamaecladum* Diels

Calandrinia sect. *Apicales* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Basales* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Tuberosae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Partitae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Pseudo-dianthoideae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Uniflorae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Parakeelya Hershk., Phytologia 84: 101. 1999 [1998].

About 74 annual and perennial species from throughout Australia, about 25 not yet described (Hancock et al. 2018; Thiele et al. 2018). All described species except *R. chamaecladum* (Diels) Ulbrich commonly remain classified *Calandrinia*. Most have combinations in *Parakeelya* (Hershkovitz 1998b, 2002; Thiele et al. 2018).

Hancock et al.'s (2018) analysis reveals partial agreement between phylogeny and classical sectional divisions, but also ambiguous relations in portions of the tree. The work also shows that perenniality evolved 2–3 times in this genus with no reversals.

Thiele et al. (2018) published a proposal to conserve the generic name *Parakeelya* [lectotype: *P. ptychosperma* (F. Muell.) Hershk.; synonym: *Calandrinia ptychosperma* F. Muell.] against *Rumicastrum*. Seddon (2005) described how he first diagnosed *Rumicastrum chamaecladum* (Diels) Ulbrich (synonym: *Atriplex chamaeclada* Diels) as a species of *Calandrinia* s. l. and not, as it had been classified, Chenopodiaceae. The latter classification owes, no doubt, to the fruit, which is achenial rather than capsulate. A fruiting specimen, lacking the ephemeral perianth and stamens and enclosed by its two sepals, indeed would resemble a female *Atriplex* flower, atepalous and enclosed by two deltoid bracts. Roger Carolin corroborated the finding (Carolin 1987, 1993; Seddon 2005) and thus planned to transfer all Australian species of *Calandrinia* s. l. to *Rumicastrum*, and he drafted a manuscript accordingly. He retired in 1986 and sent me a copy of this manuscript.

In my work (e.g., Hershkovitz 1993a), I trusted Carolin's diagnosis of *Rumicastrum*. But I had no need for a taxonomic combination in this genus until submitting my molecular phylogenetic analysis of cactus origins (Hershkovitz & Zimmer 1997) for publication. In the original journal submission, I provided a new combination for the sampled species in *Rumicastrum*. However, the journal editor, Werner Greuter (B), disputed this classification. Although the type specimen is believed to have been destroyed, he insisted that a conspecific specimen in B was "perfectly good Chenopodiaceae" and had "nothing whatsoever to do with Portulacaceae." Greuter, therefore, would not permit me to apply the name *Rumicastrum* in my publication.

I had had no means of verifying Greuter's claim, but I could not delay this publication in order to resolve a peripheral taxonomic question. Therefore, I applied a new generic name, *Parakeelya*. I learned recently that this is the same name Carolin planned to use before diagnosing the identity of *Rumicastrum* (Seddon 2005). In 1999 (nearly 20 years ago), Judy West (CANB) advised me (among other people) that Carolin's diagnosis was correct and that I had erred in erecting the genus *Parakeelya*.

Judy West and other knowledgeable Australian botanists now long have agreed that *Rumicastrum chamaecladum* is an Australian species of classical *Calandrinia* s. l. and that transfer of the remaining species was inevitable, e.g., (Richardson 1998). But they continued to classify the species in the genus *Calandrinia* – all except for one: *Rumicastrum chamaecladum*, for which no such combination in *Calandrinia* existed and none was proposed. Instead, between 2006–2017, 13 new species were described as *Calandrinia* (Obbens 2006, 2012; Syeda & Carolin 2011; West & Chinnock 2013; Obbens et al. (2017). The generic concept of *Calandrinia* in these works is not clear. Syeda & Carolin (2011) described the genus as comprising "about 100 species." At that time, there were perhaps about 55 recognized species in *Calandrinia* and *Rumicastrum* combined. The inclusion of Carolin as author was surprising, since he had advocated *Rumicastrum*. Carolin himself does not appear to have pronounced on the matter since his 1993 synopsis (Carolin 1993), which was prepared before his retirement in 1986.

Hancock et al. (2018) circumscribed *Calandrinia* as comprising this genus sensu Hershkovitz (1993a) plus *Rumicastrum*. This circumscription, which the same work rejects, appears to be *ad hoc*. It has no precedent and was not supported (though not unequivocally refuted) by prior evidence (e.g., Applequist et al. 2007; Ogburn & Edwards 2015). Hancock et al. (2018) argued that existing evidence did not prove that *Rumicastrum* was not sister to *Calandrinia*. A sister relation would justify, on phylogenetic taxonomic criteria, the continued classification of *Rumicastrum* species as *Calandrinia*. Another possibility was that the peculiar *R. chamaecladum* would figure outside of this clade. Hancock et al. (2018) rejected both possibilities.

Hancock et al. (2018) evidently knew that their ad hoc circumscription of *Calandrinia* was not monophyletic and that *Rumicastrum* was the correct name for the Australian plants. But they preferred to not apply the name *Rumicastrum*, seeking instead to conserve the name *Parakeelya*, (Thiele et al 2018), which, pending proposal resolution, remains incorrect. Unable to use *Parakeelya* and unwilling to use *Rumicastrum*, they continued to use *Calandrinia*. It is for this reason that the authors committed themselves to an a posteriori ad hoc circumscription of *Calandrinia* that they knew a priori was incorrect.

But even if these genera indeed form a clade, existing molecular evidence indicate that strong support was unlikely. Moreover, their demonstrated morphological, genetic, and biogeographic divergence rendered senseless, even misleading, their merging. To appreciate this, had the Australian plants been described initially as a new genus (and never classified in *Calandrinia* s. l.), there would seem to have been no reasonable basis (or motive) for then merging said genus with *Calandrinia*, even if the resulting genus were monophyletic, and much less so in a paper that proved that the thusly merged genus is not monophyletic.

The preceding clarified, the importance of Hancock et al. (2018) and their collaborators' research cannot be understated. Study of this genus had been badly neglected, as evidenced by the large number of new species described and predicted. Aside from their value in study of succulence, several species have ornamental value, especially with the trend towards water conserving garden plants.

3. CISTANTHEAE Hershk., **tax. nov. LECTOTYPE** (designated here): *Cistanthe* Spach.

Diagnosis. Clade of Montiaceae including the genus *Cistanthe* Spach characterized by shared DNA sequence characteristics that render them distinct from other Montiaceae.

3A. CISTANTHE Spach, Hist. Nat. Veg. 5: 229. 1836. **LECTOTYPE** (designated here): *Cistanthe grandiflora* (Lindl.) Schltdl. Synonym: *Calandrinia grandiflora* Lindl. (*nom. cons.*).

Tegneria Lilja, Fl. oefver Sver. Odl. Vext.76. 1839. **LECTOTYPE** (designated here): *Tegneria discolor* (Schrad.) Lilja. Synonyms: *Calandrinia discolor* Schrad. *Cistanthe discolor* (Schrad.) Spach. *Rhodopsis discolor* (Schrad.) Lilja. Lectotypification here of *Tegneria* Lilja is for clarification. Lilja (1841) included in this genus *Calandrinia discolor* Schrad. and, apparently erroneously, *Calandrinia speciosa* Lindley, 1833, *nom. illegit.* [synonyms: *Calandrinia elegans* Spach. *Calandrinia menziesii* (Hook.) Torr. & A. Gray. *Cistanthe speciosa* Lilja ex Heynh. (cf. Reiche 1897, 1898; Rydberg 1928)] and not *Calandrinia speciosa* Lehm., 1831 (Hershkovitz 2019a). It is the latter that pertains to *Cistanthe*, hence *Tegneria.* Lilja evidently did not appreciate that the homonymous plants were distinct (see Steudel 1840: *253*; cited by Lilja 1841). Thus, the lectotypification here establishes that *Tegneria* (hence *Rhodopsis* Lilja) are taxonomic synonyms of *Cistanthe* and not *Calandrinia*. Peralta & Ford Werntz (2008) and Hershkovitz (2018a) erroneously used the combination "*Cistanthe speciosa* (Lehm.) Lilja ex Heynh." as a synonym for *Calandrinia speciosa* Lehm. This combination does not exist. Adding further confusion is an additional homonym, *Calandrinia speciosa* Hooker, 1835, *nom. illegit.* Taxonomically, this plant is *Cistanthe laxiflora* (Phil.) Peralta & Ford-Werntz (see Hershkovitz 2019a).

Rhodopsis Lilja, Fl. Sverig. Suppl. 1: 42. 1840.

At least 38 species of succulent annual and perennial herbs, a few perennials being suffruticose/pachyform, of the ChFR (Chile, 18S–40S, Argentinean Andes, southern coastal Peru), with two species in SW North America (Ford[-Werntz] & Peralta 2002; Peralta & Ford-Werntz 2008; Hershkovitz 2018a).

Current acceptance of the generic segregation of *Cistanthe* from *Calandrinia* s. l. stems from Carolin's (1987, 1993) work. Combinations for these taxa transferred from *Calandrinia* s. l. are provided in Hershkovitz (1991b), Ford-Werntz & Peralta (2002), and Peralta & Ford-Werntz in Zuloaga et al. (2007) and below.

The current cladistic circumscription of *Cistanthe* was proposed in Hershkovitz (2006), based on molecular analysis. This work demonstrated that the circumscriptions of Carolin (1987, 1993) and (Hershkovitz 1990a, 1991a, 1992, 1993a), based on morphology, were paraphyletic. Ogburn & Edwards (2015) subsequently confirmed paraphyly of the 1990 circumscription. They did not note that their circumscription of *Cistanthe* was identical to Hershkovitz (2006).

Hershkovitz (2018a) considers that current molecular evidence demonstrates that the numerous morphological similarities shared among sections of the paraphyletic *Cistanthe* in the Hershkovitz (1990a) circumscription are symplesiomorphies, not convergences. This is supported by low genetic divergence among these taxa. Thus, these shared traits appear to reflect morphology prevalent in among "paleomonts," from which other genera have diverged markedly.

Taxonomy of *Cistanthe* remains problematic. The most recent and most comprehensive taxonomic treatment is Reiche (1898), which is more than 120 years old, and covers only the Chilean

species. It was based substantially on work of Philippi, especially Philippi (1893a, b). Reiche (1898) clearly was frustrated by this genus, combining diverse related forms as polymorphic species and manifesting uncertainty regarding the status of others. Also, numerous species have been described since Reiche's (1898) treatment.

The taxonomic difficulty is understandable. The plants are succulent and, unless carefully prepared, make poor herbarium specimens. Especially older collections, including type specimens, often are degraded and/or fragmentary and incomplete. Another problem is that most described species are endemic to the arid zone of Chile, especially between Regions II–IV. Because of the ENSO effect, periodicity of rains ranges from about 10 years to almost literally forever. This renders difficult plant exploration across this 1000 km tract. Moreover, species distributions in this area behave differently from areas of denser vegetations, which create local biotic communities and niches. Also, the stressful environment presumably induces mutation, such that odd phenotypes might be collected once and never again. The principal constraint on growth is not so much morphological phenotype as it is adequacy of moisture in the location where a seed happens to germinate. Finally, the strong moisture gradients across relatively short distances probably creates an unusual germplasm pool. In particular, in especially rainy years decades apart, the emerging plants represent correspondingly separated generations. Over historical time, the generational difference between plants emerging in a single wet year can accumulate to thousands or more years.

Hershkovitz (2018a) discussed in greater detail the taxonomy of the Chilean species. This discussion is not repeated here; it will be the subject of a spin-off work that revises and corrects errors in the account in Hershkovitz (2018a).

3A1. CISTANTHE sect. CISTANTHE.

Calandrinia sect. *Grandiflorae* Philippi, Anales Univ. Chile 178. 1893.

Calandrinia sect. *Cistanthe* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897.

At least 10 and perhaps 12 species of the ChFR, all but one perennial, primarily in Chile, one extending into San Juan Province, Argentina, and two endemic to Peru (León 2006; Peralta & Ford-Werntz 2008; Hershkovitz 2018a, d, 2019b).

Circumscription of this section corresponds almost completely to Reiche's (1898), except that Reiche referred *Cistanthe cachinalensis* (Phil.) Peralta and D.I. Ford [in my opinion, conspecific with *C. grandiflora* (Lindl.) Schlect] to his *Calandrinia* sect. *Rosulatae* (Hershkovitz 2018d). Smith et al. (2017) and Hancock et al. (2018) demonstrated that the Peruvian *C. paniculata* (Ruiz & Pav.) Carolin ex Hershk. pertains to this section. Some taxonomically necessary combinations are lacking and provided here. As in Hershkovitz (1990a, 1991b), I attribute authorship to Roger Carolin, based on an unpublished manuscript he sent me in 1986. This recognizes especially Carolin's contribution to modern Montiaceae taxonomic and phylogenetic concepts.

For expedience, I provide below taxonomically necessary combinations per Hershkovitz (2018a).

CISTANTHE AEGITALIS (F. Phil.) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia aegitalis* F. Phil., Anales Univ. Chile 85: 184. 1893. **LECTOTYPE**: **CHILE. Region IV**. Limarí Province: "Fray Jorge, litt. maris," *F. Philippi s.n.* (SGO!).

CISTANTHE CRASSIFOLIA (Phil.) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia crassifolia* Phil., Anales Univ. Chile 85: 180. 1893. **LECTOTYPE**: **CHILE. Region III**. Huasco Province: Carrizal, *F. Philippi s.n.* (SGO!).

CISTANTHE MUCRONULATA (Meyen) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia mucronulata* Meyen, Reise Erde 1: 314. 1834. **TYPE**: not located. The species was described from Chile, Region VI, Colchagua Province, in the vicinity of San Fernando. Only one species of the section grows in that region, so its identity is not in doubt.

In addition, also for expedience, I validate here the name of a new species described and analyzed in detail in the as yet not validly-published Hershkovitz (2019b).

CISTANTHE SUBSPECIOSA Hershk., **sp. nov.** **LECTOTYPE** (designated here): CHILE. Atacama Region. Tierra Amarilla Province. Tierra Amarilla: ca. 700 m elevation. September, 1924, *Werdermann 405* (E, image! <http://data.rbge.org.uk/herb/E00033178>); **ISOTYPES:** F!, U! (image! <http://data.biodiversitydata.nl/naturalis/specimen/U.1523945>), US!).

Diagnosis. Plants pertaining phylogenetically to *Cistanthe* sect. *Cistanthe*, morphologically similar to but distinct from: (1) *Cistanthe cabrerae* (Añon) Peralta and *Cistanthe grandiflora* (Lindl.) Schltdl. [incl. *C. cachinalensis* (Phil.) Peralta & D.I. Ford and probably *Calandrinia taltalensis* I.M. Johnst. in having normally 80–100 rather than ca. 50 stamens in fully developed flowers and a long (ca. 15 mm) exserted rather than shorter (< 10 mm) style; and from (2) *Cistanthe laxiflora* (Phil.) Peralta & D. I. Ford in having a herbaceous to suffruticose rather than fruticose habit, broadly ovate rather than narrowly obovate to lanceolate and more succulent leaves, and leafy inflorescence stems.

3A2. CISTANTHE sect. **ROSULATAE** (Reiche) Hershk., **comb. nov.** Basionym: *Calandrinia* sect. *Rosulatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897. **LECTOTYPE** (designated here): *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk. Synonym: *Calandrinia longiscapa* Barnéoud.

Calandrinia sect. *Arenarie* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Andinae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

At least 26 annual and perennial species, primarily of the ChFR, mainly Chile, four extending into Argentina (Peralta & Ford Werntz 2008; Hershkovitz 2018a), one primarily in Peru but now collected in Chile, one endemic to Peru (León 2006), and two in SW North America (Hershkovitz 1991a). I have collected but not forms that probably represent distinct species

Taxonomy of *C.* sect. *Rosulatae* species is woefully inadequate, especially for reasons cited above. Also, I have observed in the field three "smoking gun" cases of interspecific hybridization, i.e., where the distinct parental species and their hybrid offspring occur together (Hershkovitz 2006 and unpublished observations).

Hershkovitz' (2006) analysis indicates that *Cistanthe* sect. *Rosulatae* comprises two clades, which are recognized here as subsections.

3A2a. CISTANTHE sect. ROSULATAE (Reiche) Hershk. subsect. **ROSULATAE, subsect. nov.**

Based on Hershkovitz (2006), the discussion above, and personal communication from other researchers, I estimate that there are at least 20 species in this subsection, a few undescribed (cf. Watson 2019). It includes all species of Reiche's (1897, 1898) *Calandrinia* sect. *Andinae*. These species are mainly Chilean, with a few extending into Argentina. This section also includes several species pertinent to Reiche's *Calandrinia* section *Rosulatae* and all species pertinent to section *Arenarie*. Into the former, Reiche (1898) included *Calandrinia longiscapa* Barnéoud [synonym: *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk.], "pata de guanaco;" the most conspicuous species that essentially defines the Atacama Desert's occasional "desierto florido" phenomenon.

Watson (2019) described a new species, discovered in 2008, that he believed belongs to this subsection. Subsequently, Hershkovitz (2006: *44*, *62*) reported on later (1950s–2002) collections of this species from the type locality. Based on both plastome and nucleosome evidence, Hershkovitz (2006) also confirmed Watson's (2019) earlier phylogenetic conclusion.

Hershkovitz (2018a) described taxonomic problems in *C.* sect. *Rosulatae* subsect. *Rosulatae*, in particular consequent to his assertion that *Cistanthe arenaria* (Cham.) Carolin ex Hershkovitz is a perennial herb of south-central Chile, rather than, as had been believed, an annual species of north-central Chile. This, in turn, creates havoc with the taxonomy of the many annual forms that commonly are classified as *C. arenaria*.

The discussion in Hershkovitz (2018a) will be elaborated and corrected in a separate work. For expedience, necessary recombinations are provided below.

CISTANTHE CHAMISSOI (Barnéoud) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia chamissoi* Barnéoud in Gay, Fl. Chil. 2(4): 497–498. 1846 [1847]. Synonym: *Calandrinia arenaria* Cham. var. *chamissoi* Reiche, Fl. Chile 2: 346. 1898 and An. Univ. Chile 100: 350. 1898. **LECTOTYPE** (designated here): **CHILE. Region V**. Quillota Province. Quillota: "in petrosis sterilibus calidisque collium," *Bertero 1348,* (G: G440496, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303418&lang=en> [image!]. **ISOTYPES**: G: G440495, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303417&lang=en> [image!], G440494, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303416&lang=en> [image!], P!, P01903300, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p01903300> [image!]). **SYNTYPE**: **CHILE. Region V**. Cachapoal Province. Rancagua. *Bertero 683* (P! P01903301, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p019033001> [image). NOTE: *Bertero 683* evidently is a mixed collection that includes the type of *Talinum trigonum* Colla (see below).

CISTANTHE OBLONGIFOLIA (Barnéoud) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia oblongifolia* Barnéoud in Gay, Fl. Chil. 2(4): 482–483. 1846 [1847]. **HOLOTYPE**: **CHILE. Region IV**. Elqui Province. Llanos de Guanta: "croissant dans les endroits sablonneauxde cordilleres," *Gay 316* (P! <http://coldb.mnhn.fr/catalognumber/mnhn/p/p019033008>).

CISTANTHE TRIGONA (Colla) Hershk., **comb nov.** Basionym: *Talinum trigonum* Colla, Mem. Realle Accad. Torino 37: 71. 1834. **TYPE**: **CHILE. Region VI**. Cachapoal Province. Rancagua: "in arenososque secus flumen Cachapual," *Bertero 683* (isotypes: G, G00440471, G00440472, G00440473, G00440474, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303323&lang=en> [etc.; images!]). **NOTE**: *Bertero 683* evidently is a mixed collection that includes a syntype of *Calandrinia chamissoi* Barnéoud (see above). The G sheets are annotated by I. Peralta (MERL) as isotypes, but I have not located a specimen designated as a holotype or lectotype.

CISTANTHE VICINA (Phil.) Carolin ex Hershk., **comb. nov**. Basionym: *Calandrinia vicina* Phil., Anales Univ. Chile 85: 301. 1893. Synonym: *Calandrinia arenaria* Cham. var. *vicina* (Phil.) Reiche, Fl. Chile 2: 346. 1898 and An. Univ. Chile 100: 350. 1898. **Holotype**: **CHILE. Region Metropolitana.** Santiago Province. Renca Municipality: Cerro Renca, *Philippi s.n.* (SGO!).

3A2b. CISTANTHE sect. **ROSULATAE** (Reiche) Hershk. subsect. **THYRSOIDEAE** Hershk., **subsect. nov. LECTOTYPE** (designated here): *Cistanthe thyrsoidea* (Reiche) Peralta and D.I. Ford. Synonym: *Calandrinia thyrsoidea* Reiche, Fl. Chile 2: 342. 1898 and An. Univ. Chile 100: 342. 1898.

Five annual and one perennial species, including the Chilean *C. thyrsoidea* and *C. cephalaphora* (I.M. Johnst.), the North American *C. guadalupensis* and *C. maritima*, and probably the Peruvian *C. lingulata* (Ruiz & Pav.) Hershk. and *C. weberbaueri* (Diels) Carolin ex Hershk.

This section includes the remaining unaccounted species of Reiche's (1898) *Calandrinia* sect. *Rosulatae* except *C. cachinalensis* (see above). Monophyly of the subsection is documented in Hershkovitz (2006). Inclusion of *C. guadalupensis* is based on inspection of an ITS sequence in Genbank (FJ614057.1). In the range of ITS1 base positions 70–80, all samples of this clade share a five-base motif, "C]TCCCT[C." This aligns with a three-base motif, "C]-CTC-[C," shared by all other samples of both sections of *Cistanthe*. I refer *C. lingulata* and *C. weberbaueri* to this clade based on morphological resemblance to *C. thyrsoidea*.

The South American species are relatively small herbs with very small flowers, and I have observed cleistogamy in *C. thyrsoidea*. The North American species have larger and showier flowers, and *C. guadalupensis* is a pachycaul shrub.

3B. MONTIOPSIS Kuntze, Rev. Gen. Pl. 3(2): 14. 1898. **TYPE**: *Montiopsis boliviana* Kuntze. Synonyms: *Calandrinia cumingii* Hook. & Arn., *Montiopsis cumingii* (Hook. & Arn.) D.I. Ford.

Ca. 18 annual and perennial species of the ChFR, primarily in Chile, several extending into Argentinean Andes, one annual extending also into the Central Andes in Bolivia (Ford 1992; Peralta & Ford-Werntz 2008).

Hancock et al.'s (2018) 297-loci phylogenomic analysis confirms the results of Ogburn & Edwards (2015) in placing *Montiopsis* within Cistantheae. The relations of *Montiopsis* were unresolved in Hershkovitz (2006). Interestingly, Hancock et al.'s (2018) Bayesian analysis of phylogenetic concordance among loci showed significant residual support for monophyly of *Cistanthe* with Calyptridinae, as in morphological analyses of Carolin (1987) and Hershkovitz (1991a, 1993a). I hypothesize that this residual support reflects loci related to the morphological similarities of these taxa.

Hershkovitz' (1993a) cladogram shows *Montiopsis* as sister to *Calandrinia*. However, he noted that this was supported only by the shared presence of trichomes, and that the trichomes were structurally very different. He also noted the gross similarity between the acaulescent *Montiopsis* (subg. *Dianthoideae*) *cistiflora* (Gillies ex Arn.) D.I. Ford and species of *Calandrinia* sect. *Caespitosae*. The former has a 1–3-flowered axillary inflorescence, and the latter are 1-flowered, although I have seen a rudimentary second flower on a single specimen of *Calandrinia acaulis*. However, Hershkovitz (1993a) noted that inflorescence development and form of *Montiopsis* (bostryx or botryoid) otherwise was distinct from *Calandrinia* (solitary/axillary and so-derived) and *Cistanthe*

(cincinnoid). Thus, current molecular evidence confirms that the distinctive morphology of *Montiopsis* reflects its marked evolutionary divergence, as evident in branch lengths in molecular phylograms of Hancock et al. (2018).

3B1. MONTIOPSIS subg. **MONTIOPSIS**

Calandrinia sect. *Hirsutae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Condensatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 503. 1897.

Calandrinia sect. *Parviflorae* Reiche, Ber. Deutsch. Bot. Ges. 15: 503. 1897.

Calandriniopsis Franz, Bot. Jarhb. Syst. 42, Beibl. 97: 19. 1908.

Ca. 15 annual and perennial species, of the ChFR, primarily in Chile, several extending into Argentina, one extending also into Bolivia (Ford 1992; Peralta & Ford-Werntz 2008).

Existing molecular data show (Hershkovitz 2006) show no phylogenetic structure among these species.

3B2. MONTIOPSIS subg. **DIANTHOIDEAE** (Reiche) D.I. Ford, Phytologia 74: 277. 1993. *Calandrinia* sect. *Dianthoideae* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897. **LECTOTYPE**: *Montiopsis cistiflora* (Gillies ex Arn.) D.I. Ford. Synonym: *Calandrinia cistiflora* Gillies ex Arn.

At least three perennial species of the ChFR, apparently all three in Chile and the adjacent Argentinean Andes (Ford 1992: Peralta & Ford-Werntz 2008).

Molecular evidence (Hershkovitz 2006; Ogburn & Edwards 2015) demonstrates that this subgenus is monophyletic, defusing a suggestion by Hershkovitz (1993a) that it might be paraphyletic with respect to *M.* subg. *Montiopsis.*

3C. CALYPTRIDINAE Hershk., **tax. nov. TYPE**: *Calyptridium* Nutt. in Torrey & A. Gray.

Diagnosis. Clade of plants pertaining to Montiaceae-Cistantheae sharing leaf morphological and inflorescence branching traits with *Cistanthe* Spach but distinct from *Lenzia* Phil.

Except for the sister relation between *Lenzia* and remaining Calyptridinae, phylogenetic relations among the three genera remain poorly resolved (Hershkovitz 2006; Guilliams 2009). Morphology and DNA weakly support monophyly of the bicarpellate species of *Calyptridium*. Monophyly of 2–3-carpellate *Philippiamra* is not well supported, but this owes to lack of molecular divergence among the taxa. *Calyptridium* and *Philippiamra*. The problematic taxon is the three-carpellate species currently classified as *Cistanthe ambigua* (S. Watson) Carolin ex Hershk., which, on biogeographic grounds, seems to be most likely sister to the two-carpellate *Calyptridium*. Existing molecular data cannot confirm this. The present work segregates this species into its own genus.

On the basis of morphology, both Carolin (1987, 1993) and Hershkovitz (1990a, 1991a, 1993a) classified *Calyptridium* and *Philippiamra* as separate sections of *Cistanthe*. Clarification of the relations of *Lenzia* (Hershkovitz 2006) and *Montiopsis* (Ogburn & Edwards 2015; Hancock et al.

2018) defused this classification. As described above, however, the morphological similarities between these genera and *Cistanthe* appear to be symplesiomorphies and not convergences. Morphologically, *Lenzia* and *Montiopsis* are unique and highly divergent. Thus, the cladistic interpretation based on morphology is not surprising and, in a sense, is confirmed.

3C1. CALYPTRIDIUM Nutt. in Torr. & A. Gray, Fl. N. Amer. 1(2): 198. 1838. *Cistanthe* sect. *Calyptridium* (Nutt. in Torr. & A. Gray) Hershk., Phytologia 68: 267. 1990. **TYPE**: *Calyptridium monandrum* Nutt. in Torr. & A. Gray. Synonym: *Cistanthe monandra* (Nutt. in Torrey & A. Gray) Hershk.

Spraguea Torr., Smithsonian Contr. Knowl. 6: 4. 1853.

Current classifications recognize nine annual and perennial species plus three additional subtaxa of W North America (Hinton 1975; Guilliams 2009; Simpson et al. 2010; Guilliams et al. 2011; Guilliams & Miller 2014). All but one subspecific taxon occur in California. Simpson et al. (2010) argued for retaining subspecific status for four taxa of *Calyptridium parryi*, but given their allopatry and morphological distinctions, specific recognition may be warranted (see below). This would bring the species total to 12.

Molecular data (Hershkovitz 2006, 2018a; Guilliams 2009; Ogburn & Edwards 2015) evidence two clades in the genus corresponding to the morphological distinctions of the species referable to the segregate genus *Spraguea* and the remaining species of *Calyptridium* (Hershkovitz 1991a, b). Thus, *Calyptridium* here is divided into two sections.

3C1a. CALYPTRIDIUM sect. CALYPTRIDIUM

Six to nine annual species of SW USA and NW Mexico.

The species share the derived two-carpellate condition with *C.* sect. *Spraguea* and otherwise the pleisiomorphic vegetative and reproductive traits of other Calyptridinae and species of *Cistanthe* (Hershkovitz 1991a, b, 2018a). Simpson et al. (2010) argued for retention of subspecific status for three traditionally recognized varieties of *C. parryi*. Nonetheless, the varieties are distinguished easily geographically, ecologically, and morphologically. In current Montiaceae taxonomies, subspecific taxa seem to be eschewed in all genera except this one, *Claytonia*, and *Lewisia*. Subspecific taxa have been named in other genera, but current taxonomists seem to prefer to lump with or split from their species. Subspecific taxa of *Claytonia* generally manifest intergradation and or gene flow (Miller & Chambers 2006, 2012; McIntyre 2012, Stoughton et al. 2017a, b), as do those of some *Lewisia* species (Hershkovitz & Hogan 2002a, b). But I have recommended that allopatric and distinct entities be recognized as species, and by that criterion, all *Calyptridium parryi* subtaxa qualify. The main argument against this is in the interest of conserving well-established usage. As ever, much of taxonomy is aesthetics and ergonomics.

I provide here in brief form recombinations as species for remaining *Calyptridium parryi* subtaxa.

CALYPTRIDIUM HESSAE (J.T. Thomas) Hershk., **comb. et stat. nov.** Basionym: *Calyptridium parryi* A. Gray var. *hessae* J.T. Thomas, Leafl. W. Bot. 8: 10. 1956. Synonym: *Cistanthe parryi* (A. Gray) Hershk. var. *hessae* (J.T. Thomas) Kartesz & Ghandi, Phytologia 71: 62. 1991.

CALYPTRIDIUM MARTIRENSE (Guilliams, M.G. Simpson & Rebman) Hershk., **comb. et stat. nov.** Basionym: *Calyptridium parryi* A. Gray var. *martirense* Guilliams, M.G. Simpson & Rebman, Madroño 58: 260. 2012 ["2011"].

CALYPTRIDIUM NEVADENSE (J.T. Howell) Hershk., **comb. et stat. nov.** Basionym: *Calyptridium parryi* A. Gray var. *nevadense* J.T. Howell, Leafl. W. Bot. 4:216. 1945. Synonyms: *Calyptridium parryi* A. Gray subsp. *nevadense* (J.T. Howell) Munz, Fl. S. Calif. 711. 1974. *Cistanthe parryi* (A. Gray) Hershk. var. *nevadense* Kartesz & Ghandi, Phytologia 71: 62. 1991.

3C1b. CALYPTRIDIUM sect. SPRAGUEA (Torr.) Hershk., **comb. et stat. nov.** *Spraguea* Torr., Smithsonian Contr. Knowl. 6: 4. 1853. **LECTOTYPE** (designated here): *Calyptridium monospermum* Greene. Synonym: *Cistanthe monosperma* (Greene) Hershk.

Three species, two perennial (one may behave as a winter annual) and one annual of SW USA.

Morphological evidence for sectional monophyly includes nonsucculence of the leaves, absence of planar leaf venation, and absence of the smaller of the two bracts subtending the flowers in other species (Hershkovitz 1991a, b). Molecular evidence confirms that perenniality is derived in *Calyptridium*. Although less clear, it is possible that the lower elevation and more ephemeral condition of *C. monospermum* represent an evolutionary reversal from the alpine and longer-lived condition of *C. umbellatum* (Torr.) Greene. The reduction of seed number to one in *C. monospermum* suggests that this species is derived. The two species hybridize and introgress in at least some locations along their ca. 1000 km contact zone (Hinton 1975).

3C2. THINGIA Hershk., **gen. nov. LECTOTYPE** (designated here): **THINGIA AMBIGUA** (S. Wats.) Hershk., **comb. nov.** Basionym: *Claytonia ambigua* S. Watson, Proc. Amer. Acad. Arts 17: 365(–366). 1882. Synonyms: *Calandrinia ambigua* (S. Watson) Howell, Erythea 1: 34. 1893. *Cistanthe ambigua* (S. Watson) Carolin ex Hershk., Phytologia 68: 269. 1990.

Diagnosis. Montiaceae-Cistantheae-Calyptridinae differing in having the combination of three carpels and three-dimensional basket-like leaf venation.

Description. Plants annual, rosettiform with branched inflorescences, leaves succulent with three-dimensional leaf venation, the marginal veins connecting to form a "basket," inflorescence a sub-umbellate cincinnus, flowers many, pedicellate, subtended by a pair of markedly unequal scarious bracts, sepals 2, petals 5, stamens 5, carpels 3, fruit capsulate with 3 valves, dehiscence basipetal, seeds several, black, smooth, shiny, embryo peripheral, nearly circular.

One species of the Mojave and Sonoran Deserts, Arizona, California, and adjacent northwestern Mexico (Guilliams 2009).

Etymology. The generic name metaphorically refers to one of the colloquial names for the type species, "dead man's fingers" (SEINet 2018). Thus, the genus is named for the literary figure, Thing, of the Addams Family cartoon, television series, and movie. "Thing" is an animated but (at least in the movie) disembodied human hand. This suggests that the hand derives from a deceased human, hence possesses "dead man´s fingers." The generic combination also suggests an appropriate

vernacular name, "ambiguous thing," reflecting the ambiguity of the status of this species following cladistic classification of Montiaceae.

Kelley (1973) classified this species in *Calandrinia* sect. *Amarantoideae* Reiche, a synonym of *C.* sect. *Amarantoidae* Philippi, here classified in *Philippiamra* (see below). Hershkovitz (1990a, 1991a, 1993a) effectively followed Kelley (1973), transferring the species to *Cistanthe* sect. *Amarantoideae* (Reiche) Carolin ex Hershk. As noted above, molecular data have not established its position within Calyptridinae. The segregation renders *Calyptridium* and *Philippiamra* more homogeneous morphologically, genetically, and/or biogeographically. It also conserves as best as possible existing taxonomic usage in the sense that this species conventionally was classified in *Calandrinia* s. l. or, more recently, in *Cistanthe*., i.e., always in a genus separate from *Calyptridium*.

An earlier incarnation of this work (2018a) and earlier circulated draft of this same work classified this taxon two ways, as a separate genus and as a section and species of *Calyptridium*, allowing users (e.g., flora editors) to select their preference. Editor Guy Newsom pointed out that this violates the Article 36 proscription of designating taxa in anticipation of their eventual acceptance (McNeill et al. 2012). Article 36 is problematic, because taxonomy is democratic, not authoritarian. *All* formal taxon designations, without exception, merely anticipate and in no instance obligate taxon acceptance. The only function of the Code is to establish conventions for proposing taxon names, establish the semantic meaning of validated names, and establish priority of taxon types and authorships. Nothing in the code prohibits multiple classifications of the same type, as in Hershkovitz (2018a), except in *separate* publications.

More to the point, the Code takes no account of Heisenberg's mathematical Uncertainty Principle, nor the related wave-particle duality/ambiguity in quantum physics. I described above the "wave model" of species, which suggests that the mathematical/ physical phenomenon is applicable to taxonomy, i.e., that there exists a wave-taxon duality, such that taxa instantaneously interchange between multiple ontologies, hence cannot be simultaneously observed and classified. Corroborating this, it was Sereno Watson, not me, that named this species *ambigua*. This phenomenon, the *Taxonomic* Uncertainty Principle, emerges as a lemma of the wave model of species.

3C3. PHILIPPIAMRA Kuntze, Rev. Gen. Pl. 1: 58. 1891. *Silvaea* Phil., Fl. Atacam. 21. 1860 (*non Silvaea* Hook. & Arn., Bot. Beech Voy. 211. 1837). *Cistanthe* sect. *Philippiamra* (Kuntze) Hershk., Phytologia 68: 269. 1990. **LECTOTYPE** (designated here): *Philippiamra pachyphyllum* (Phil.) Kuntze. Synonyms: *Silvaea pachyphylla* Phil. *Cistanthe pachyphylla* (Phil.) Carolin ex. Hershk.

Calandrinia sect. *Amarantoidae* Philippi, Anales Univ. Chile 85: 172. 1893.

Calandrinia sect. *Amarantoideae* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897. *nom. superfl.*

Cistanthe sect. *Amarantoideae* (Reiche) Carolin ex Hershk., Phytologia 68: 269. 1990. *comb. illegit.*

Perhaps 10 annual species of ChFR Atacama Desert region, Chile, 18S–28S, extending to adjacent Argentinean Andes (Hershkovitz 1991a; Peralta 1999; Peralta & Ford-Werntz 2008).

Taxonomy of *Philippiamra* is even more difficult than that of *Cistanthe*, for the reasons cited above and more. The genus is distributed mainly in the hyperarid zone of Chile's Regions II and III, extending to the northern province of Region IV. The exploration difficulty posed by infrequent rain

thus is exacerbated. Also, the flowers are much smaller than those of *Cistanthe*. Because of their succulence, herbarium specimens often break and crumble.

Philippiamra includes both three-carpellate, capsulate, multiple-seeded species formerly classified in *Calandrinia* s. l. and two-carpellate achenial species classified in *Philippiamra*. Existing molecular data do not discriminate between these groups (Hershkovitz 2006). Both ribosomal and plastid genotypes are shared indiscriminately among both forms.

I have observed that in El Ñino "desierto florido" years, *Philippiamra celosioides* (Phil.) Kuntz is the last plant encountered when approaching the driest and rain-free sector of the Atacama Desert in Region II of Chile, E/SE of Antofagasta. Retreating from here, other *Philippiamra* species appear along with species of *Cistanthe* sect. *Rosulatae*. Bahamondes et al. (2012) described a desolate habitat N/NE of Antofagasta harboring only *P. salsoloides*. Thus, *Philippiamra* may include the world's most drought-tolerant vascular plant species.

According to Brummit (1993), *Philippiamra* replaced *Silvaea* Phil., which had been deemed a homonym with an earlier generic name, *Silvia* Benth. (Scrophulariaceae). Brummit reported that the nomenclatural committee deemed the two names distinct and concluded that "*Silvaea* should be adopted in Portulacaceae and *Philippiamra* should be regarded as a superfluous substitute." Strangely, no reference was made to another earlier generic name, *Silvaea* Hook. & Arn. (Euphorbiaceae). The latter appears to be legitimate and valid (Webster 1994), hence *Silvaea* Phil. remains homonymous and should be considered illegitimate.

Carolin (1993) included the genus *Diazia* in *Philippiamra* as circumscribed here. I have referred *Diazia* to *Calandrinia* (see above).

I provide here taxonomically necessary combinations in brief format:

PHILIPPIAMRA ARANCIOANA (Peralta) Hershk., **comb. nov.** Basionym: *Cistanthe arancioana* Peralta, Gayana Bot. 52: 45. 1995.

PHILIPPIAMRA CALYCINA (Phil.) Hershk., **comb. nov.** Basionym: *Calandrinia calycina* Phil., Fl. Atacam. 21. 1860. Synonym: *Cistanthe calycina* (Phil.) Carolin ex Hershk., Phytologia 70: 220. 1991.

PHILIPPIAMRA DENSIFLORA (Barnéoud) Hershk., **comb. nov.** Basionym: *Calandrinia densiflora* Barnéoud in Gay, Fl. Chil. 2(4): 503. 1846 [1847]. Synonym: *Cistanthe densiflora* (Barnéoud) Carolin ex Hershk., Phytologia 70: 220. 1991.

PHILIPPIAMRA MINUSCULA (Cullen) Hershk., **comb. nov.** Basionym: *Calandrinia minuscula* Cullen, Bol. Soc. Arg. Bot. 5: 12. 1953. Synonym: *Cistanthe minuscula* (Cullen) Peralta in Kiesling, Fl. San Juan 1: 163. 1994

PHILIPPIAMRA SALSOLOIDES (Barnéoud) Hershk., **comb. nov.** Basionym: *Calandrinia salsoloides* Barnéoud in Gay, Fl. Chil. 2(4): 502–503. 1846. Synonym: *Cistanthe salsoloides* (Barnéoud) Carolin ex Hershk. in Phytologia 68: 269. 1990.

3C4. LENZIA Phil., Linnaea 33: 222. 1864. **LECTOTYPE** (designated here): *Lenzia chamaepitys* Phil.

One perennial species of the ChFR: Chile, Regions III and IV, and adjacent Argentinean Andes, above 3000 m (Hershkovitz 2006).

As noted in Hershkovitz (2006), this peculiar acaulescent and evidently finely rhizomatous plant bears no obvious morphological similarity to other Calyptridinae (Reiche, 1898). The plant appears as a ca. 2 cm long cone of scarious-margined awl-shaped leaves. The mesophyll occupies only a thin central portion of the leaf. Flowers are axillary, solitary, with scarious bracts. Found between 3000–4000 m on Andean slopes, it evidently is resistant to extremes of both high and low temperatures and high (i.e., snowmelt) and low moisture.

4. PHEMERANTHEAE Hershk., **tax. nov. TYPE**: *Phemeranthus* Raf.

Diagnosis. Distinct from other Montiaceae in having the combination of a dichasial inflorescence and leaves with 3-dimensional venation and basal appendages that clasp the stem.

Molecular/phylogenomic analyses show *Phemeranthus* as sister to remaining Montiaceae (see above), but *Schreiteria*, here included in Phemerantheae, has not been sampled and possibly is extinct.

4A. PHEMERANTHUS Raf., Specchio Sci. 1: 86. 1814. *Talinum* sect. *Phemeranthus* (Raf.) DC., Prodr. 3: 356. 1828. **TYPE**: *Phemeranthus teretifolium* (Pursh) Raf. Synonym: *Talinum teretifolium* Raf.

About 25 perennial species, mainly in North American, one in Argentina (Ferguson 2001, Price 2012). *Phemeranthus confertiflorus* (Greene) Hershk. is adventive in Europe (Nagodă et al. 2013).

The largely North American distribution of the species intriguing. All Portulacineae outgroups of Montiaceae appear to have southern hemisphere origins, as do other early diverging Montiaceae. Thus, *Phemeranthus* may have waifed to North America prior to the diversification of remaining Montiaceae. Alternatively, as noted above, it is not inconceivable that South American Montiaceae arrived by dispersal from North America. Phylogenetic relations among *Phemeranthus* species remain poorly resolved (Price 2012). Interestingly, the Argentinean species diverges early in the cladogram. Resolution of *Phemeranthus* origins may be contingent upon the relations of the Argentine-endemic *Schreiteria* (see below).

4B. SCHREITERIA Carolin, Parodiana 3: 330. 1985. **TYPE**: *Schreiteria macrocarpa* (Carolin) Speg. Synonym: *Calandrinia macrocarpa* Speg.

One species of Tucumán Province, Argentina.

As far as I can determine, the species is known only from the type collection. Carolin's (1987) morphological analysis found the monotype to be sister to *Talinum* s. stricto. But the leaf venation is three-dimensional and the leaf base is pseudo-clasping, as in all species of *Phemeranthus* (Hershkovitz 1991c; Ogburn & Edwards 2013). The essentially sessile leaf is prominently constricted at the base into a miniscule petiole. A false clasping leaf base is formed by basal extension of the succulent leaf blade.

Abbreviations. CCM, carbon concentrating mechanism; CFP, California Floristic Province; ChFR, Chilean Floristic Region; CPR, Cape Floristic Region; ITS: nuclear ribosomal DNA internal

transcribed spacer; LDD: long-distance dispersal; MAP: mean annual precipitation; WGD: whole-genome duplication

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VERBENA JESSICAE (VERBENACEAE), A NEW SPECIES FROM NUEVO LEÓN, MEXICO

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ABSTRACT

Verbena jessicae Nesom & Hinton, **sp. nov.**, is described from a gypseous llano in northeastern Nuevo Leon, Mexico. It grows closely intermixed with another local endemic, *Glandularia alejandrana*, and with the widespread *Verbena canescens*. The new species is characterized by its small, pinnately divided leaves, hirsute and stipitate-glandular vestiture, small, salverform flowers with apically notched petals, and especially by its procumbent to decumbent habit and short, few-flowered, solitary spikes.

Continued floristic exploration of gypseous areas in northeastern Mexico has brought to light a previously undescribed species of *Verbena*.

VERBENA JESSICAE Nesom & G.S. Hinton, **sp. nov.** **TYPE**: **MEXICO**. **Nuevo León**. Mpio. Galeana: Rancho Aguililla, gypseous llano in broad valley S of San Rafael, 2950 m, common over a few hectares, flowers purple, decumbent, 31 Mar 2010, *G.S. Hinton et al. 29086* (holotype: TEX; isotypes: ANSM, GBH, MEXU). Figures 1–6.

Similar to *Verbena canescens* but distinct in its small, pinnately divided to deeply toothed leaves, hirsute and stipitate-glandular vestiture, salverform corollas, and particularly in its procumbent to decumbent habit and short, terminal, few-flowered spikes.

Annual to short-lived perennial herbs, taprooted. **Stems** 3–10 from the base, procumbent to decumbent, not rooting at nodes, 2–10 cm long, ascending at the spike apices, densely hirsutulous with hairs mostly 0.1–0.2 mm long, stipitate-glandular with subsessile glands to 0.2 mm. **Leaves** mostly broadly ovate in outline, to oblong-oblanceolate or oblong-lanceolate, pinnately divided to deeply toothed, (2–)3–5 lobes or teeth per side, the divisions oblong-linear to lanceolate-linear, antrorsely directed, lower and midstem 5–10(–15) mm x 2 x 5 mm, hirsute-strigose to strigose-hirsute on both surfaces and stipitate-glandular with subsessile glands, veins impressed adaxially, margins narrowly revolute, blades basally attenuate but without a distinct petiolar region. **Fruiting spikes** terminal or axillary, 6–10 mm long, barely elongating, with 5–12 fruits; floral bracts linear-lanceolate to lanceolate, 2.5–3.5 mm, shorter than the calyces. **Calyces** (3–)3.5–4 mm, subcylindric, hirsute to hirsutulous, stipitate-glandular, lobes narrowly lanceolate, erect, connivent. **Corollas** violet to light purple or nearly white, salverform, tubes 3–3.5 mm, 1–1.5 mm longer than the calyces, limbs 2–3 mm in diam, petals notched at the apices. **Nutlets** 1.8–2.2 mm, easily separating; commissural faces not reaching nutlet apices, white-bullate.

Additional collections. **Nuevo León**. Mpio. Galeana: San José del Alamito to El Coyote, grassy gypseous llano, 1780 m, procumbent, flowers purple, very small, 15 Jul 1998, *G.S. Hinton et al. 27202* (GBH, TEX); roadside Hwy 57, near Puerto México, grassy llano, 1900 m, flowers purple, 5 cm, Sep 21, 2006, *G.B. Hinton et al. 28428* (GBH, TEX).

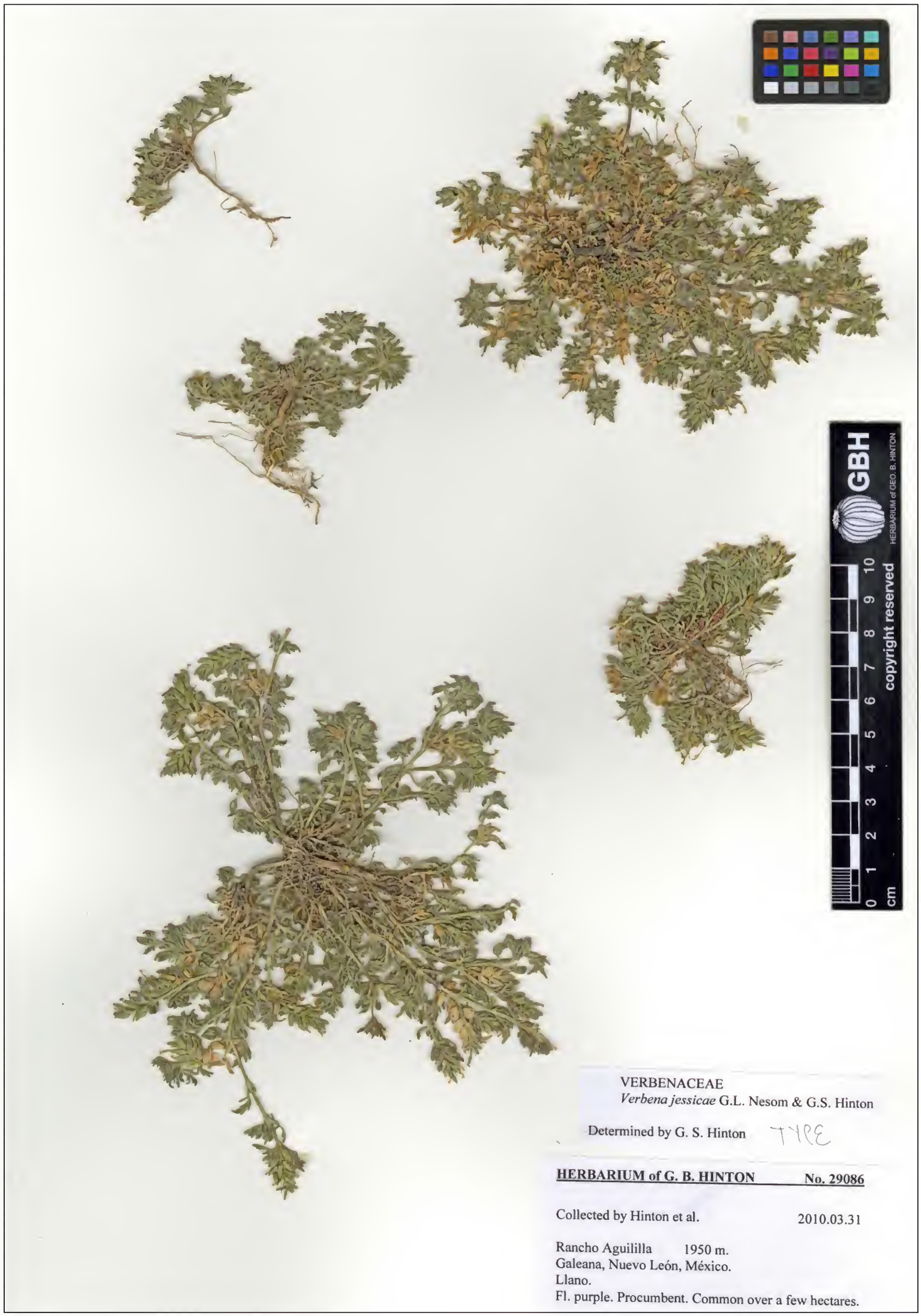

Figure 1. *Verbena jessicae*, isotype (GBH).

Figure 2. *Verbena jessicae*, dissected leaves and short, terminal and axilllary inflorescences. From *Hinton 28428* (GBH).

Figure 3. *Verbena jessicae* — vestiture and revolute leaf margins. From *Hinton 29086*.

Figure 4. *Verbena jessicae* — vestiture showing minute glandularity. From *Hinton 29086*.

Figure 5. *Verbena jessicae*, at the type locality.

Figure 6. *Verbena jessicae*, at the type locality.

Figure 7. *Verbena jessicae*, at the type locality.

Figure 8. *Verbena jessicae* (right) and *Glandularia alejandrana* (left), at the type locality of *V. jessicae*. Note the distinct corolla sizes.

Verbena jessicae is named for Jessica Hinton, daughter of the collector and frequent companion on his walks about their home in Rancho Aguililla. It grows in the same habitat and closely intermixed with *Glandularia alejandrana* B.L. Turner (Turner 1999; see Fig. 6 below), named for the collector's wife. With the description of this new species of *Verbena*, wife and daughter are twice united.

The new species grows abundantly in a broad, flat, gypseous area without shrubs (a llano). Plants in the llano tend to cluster, leaving large portions of bare soil. The islands of plants primarily include *Stipa clandestina* with *Glandularia alejandrana*, *Glandularia pinnatifida*, *Verbena canescens*, *Nama hispidum*, *Townsendia mexicana*, *Solanum eleagnifolium*, *Sphaceralcea hastulata*, *Peganum mexicanum*, and *Cryptantha gypsophila*. *Glandularia alejandrana* is known from other populations in the same region of Nuevo León and slightly westward in Zacatecas (as cited and mapped by Turner 1999).

Verbena jessicae is a member of the *V. neomexicana* Small complex (Nesom 2010b), circumscribed as *Verbena* sect. *Verbena* series *Tricesimae* Nesom (Nesom 2010a). Plants of this group generally have slender, usually solitary or few-branched spikes with remote fruits, glandular rachises and calyces, distinctly exserted corolla tubes, nutlets with commissural faces not reaching the apex, and glossy-surfaced leaves that usually are elongate and pinnatifid to deeply toothed (but varying to subentire) and with impressed venation adaxially and revolute margins. Within ser. *Tricesimae*, *V. jessicae* is distinct in its small, mostly pinnately divided leaves with linear lobes, stipitate-glandular vestiture, salverform corollas, and especially in its procumbent to decumbent habit and few-flowered spikes. The short, nearly head-like spikes, of only 5–12 flowers at the slightly upturned ends of prostrate branches, are unique in their reduction among all species of the genus.

Verbena jessicae grows closely intermixed with *V. canescens* Kunth, also of ser. *Tricesimae*––the latter is distinct in it erect habit, more dissected leaves, funnelform corollas, and elongate floral bracts. Both species are abundantly present but intermediates between them are not encountered. The new species is similar in general aspect to *Glandularia alejandrana*, which has dissected leaves

with linear lobes and few-flowered, relatively compact inflorescences, but the latter has larger plants and flowers (Fig. 6) and the fruit morphology is characteristic of *Glandularia* rather than *Verbena*.

The only other species of ser. *Tricesimae* with prostrate stems is *Verbena gracilis* Desf., a species primarily of the central and western Mexico to the southwestern USA. The closest geographical approach of *V. gracilis* to *V. jessicae* is in San Luis Potosí, where the plants often are suberect. Despite similarities in habit and leaf morphology, the two are distinct in a number of easily discernible features, as in the contrasts below.

1. Stems 2–10 cm, densely hirsutulous with hairs mostly 0.1–0.2 mm long; fruiting spikes slightly upturned, 6–10 mm long, of 5–12 fruits; floral bracts 2.5–3.5 mm, shorter than the calyces; calyces (3–) 3.5–4 mm, lobes narrowly lanceolate; petal apices notched; nutlets 1.8–2.2 mm ..... **Verbena jessicae**

1. Stems 10–25 cm, hirsute with bristly hairs mostly 0.3–0.8 mm long; fruiting spikes erect, 50–100 (–150) mm long, of 20–70 fruits; floral bracts 3–5(–8 proximally) mm, distinctly longer than the calyces; calyces 2–2.5 mm, lobes deltate to deltate-apiculate; petal apices entire; nutlets 1.5–1.8 mm ..... **Verbena gracilis**

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A NEW SPECIES OF *CHAPTALIA* (ASTERACEAE) FROM OAXACA, MEXICO

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ABSTRACT

Two collections of *Chaptalia* from southeastern Oaxaca are described as **Chaptalia exazurea** Hinton & Nesom, **sp. nov.** It is most closely related to four other Mexican species of sect. *Chaptalia* — *C. estribensis*, *C. lyratifolia*, *C. hidalgoensis*, and *C. hintonii* and is keyed in the context of those as well as the whole section. A map and illustrations are provided.

In an earlier study of *Chaptalia* (Nesom 1995), a collection from Cerro Azul in southeastern Oaxaca was identified as a long-disjunct population of *C. estribensis* Nesom, which otherwise is endemic to Hidalgo and adjacent Veracruz. Hinton (GSH) recognized that a second collection of the same entity from southern Oaxaca exists and that together the Oaxacan plants are morphologically distinct from *C. estribensis*. This is confirmed in the present study and the Oaxacan plants are formally described and named below as *Chaptalia exazurea*.

Chaptalia exazurea, *C. estribensis*, *C. lyratifolia* Burkart, *C. hidalgoensis* Cabrera & Nesom, and *C. hintonii* Bullock comprise a strongly defined group of Mexican species marked by their rhizomatous, colonial habit, cordate leaf bases, bisexual flowers with sterile ovaries, and pistillate flowers with markedly foreshortened style branches. Additionally, the ligules are whitish with (except in *C. exazurea*) a purple abaxial midstripe and the achenes unbeaked and pubescent over the whole surface with short, inflated trichomes. These have been placed as a subgroup within sect. *Chaptalia* (Nesom 1995, 2004; Cabrera & Nesom 2003).

Morphological distinctions among these five species are not great (see key below) but consistent. Each has a discrete geographic range, not overlapping any of the other four (Figure 3).

CHAPTALIA EXAZUREA G.S. Hinton & Nesom, **sp. nov. TYPE**: **MEXICO**. **Oaxaca**. Mpio. San Juan Ozolotepec: La Sirena, mixed forest, colony on cliff, 2525 m, 23 Oct 1995, *Hinton et al. 26408* (holotype: TEX; isotypes: ANSM, GBH). Figures 1, 2.

Similar to *Chaptalia hintonii* in its strongly graduated phyllaries but different in its coriaceous leaf blades with tawny undersurface and lyratiform extensions at the base and its greater number of ray flowers; similar to *C. estribensis* in its slightly retrorse marginal teeth, relatively broad involucres, and 22–28 ray flowers but different in its lyratiform leaf bases, even-length phyllaries, shorter, white ray corollas with narrower ligules, and shorter achenes.

Plants colonial through rhizomes. **Scapes** 16–20 cm tall, ebracteate. **Leaves** coriaceous, glabrescent above, densely and closely matted-tomentose below, blades ovate to obong-ovate, 3–7 cm long, 2.5–5 cm wide, base cordate, margins shallowly dentate-serrate to widely crenate with apiculate, slightly retrorse teeth, narrowly revolute; petiole sharply delimited, as long or longer than the blade, bare or narrowly winged or sometimes with lyratiform extensions below the blade base. **Involucres** 14–16 mm wide (pressed); phyllaries 13–14 mm long, in ca. 3 series of even to subequal length, margins minutely glandular. **Pistillate flowers** in 2 series, those of the inner with ligules absent or greatly reduced; ligulate pistillate flowers 22–28 in 1(–2) series, small staminodes sometimes present, corollas 9.5–12.5 mm long, ligules 0.8–1.3 mm wide, white and apparently without a purple midstripe. **Bisexual**

flowers with sterile ovaries. **Fertile achenes** not beaked, 2–2.5 mm long, pubescent over the whole surface with inflated, apiculate to blunt-tipped trichomes.

Additional collection examined. **Oaxaca**. [Mpio. Santa María Chimalapa:] Cerro Azul, cima, cerca del Rio Grande, al N de Niltepec, 2100 m, 7 Mar 1956, *MacDougall s.n.* (CAS, MEXU). Cerro Azul is one of the two main peaks of the Sierra Atravesada, about 18 mi NE of Niltepec. The two collections of *Chaptalia exazurea* are about 180 miles apart, suggesting that localities exist between them.

Figure 1. *Chaptalia exazurea* details. Top: pubescent surface of fertile achene. Middle: short style branches of ligulate pistillate flower. Bottom: glandular margins of phyllary. Photos by G.S. Hinton.

Figure 2. *Chaptalia exazurea*, GBH isotype (using mounting paper with TEX logo).

Figure 4. Chaptalia *exazurea* from Cerro Azul, northeast of Niltepec, Oaxaca. *McDougall s.n.*, MEXU.

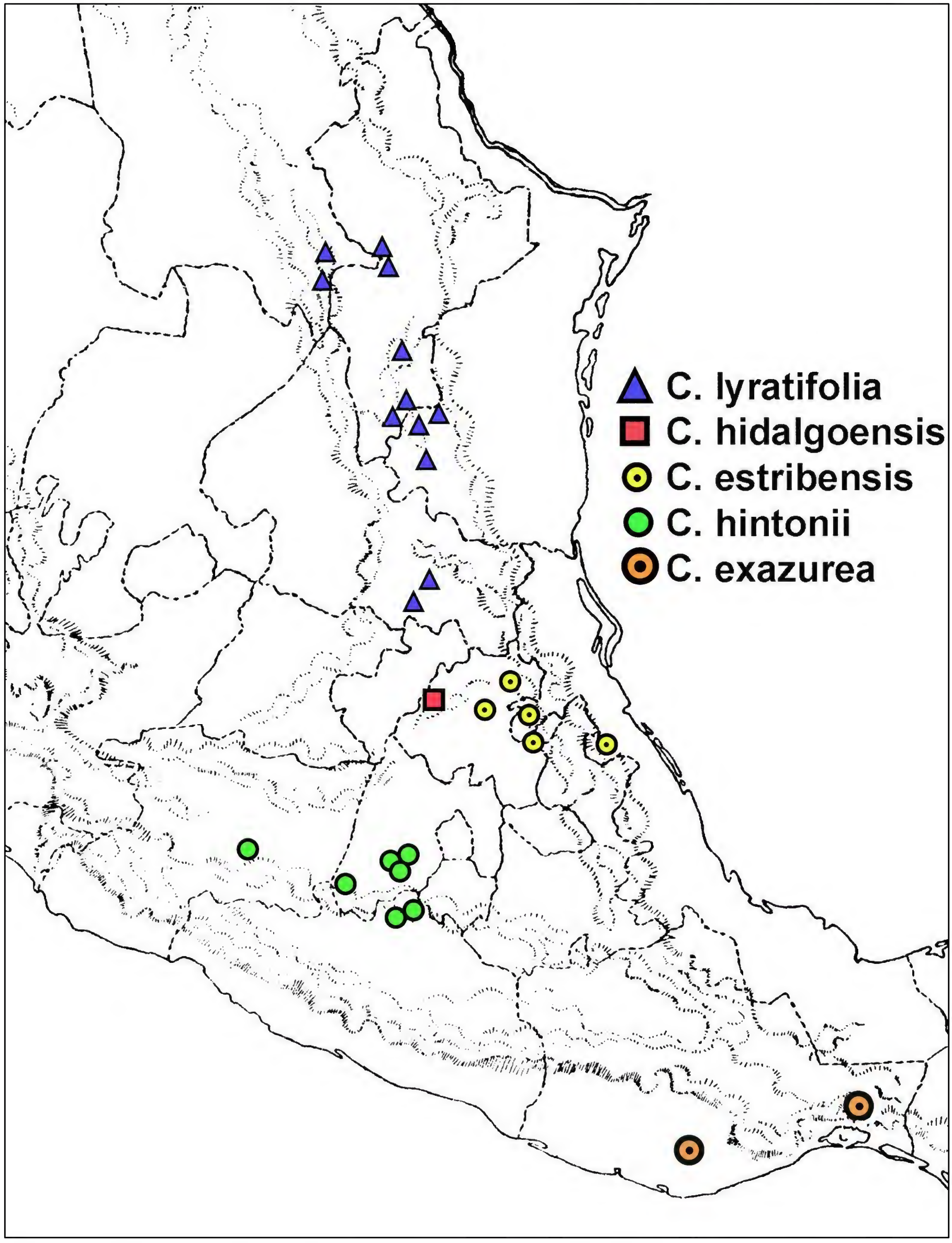

Figure 3. Distribution of the cordate-leaved species of sect. *Chaptalia*.

Figure 5. *Chaptalia estribensis*, holotype.

Synoptic key to the species of sect. *Chaptalia*

1. Leaves basally attenuate; plants without rhizomes, occurring individually.

2. Scapes bracteate; achenes fusiform or with only a short, slightly constricted neck

3. Pistillate florets in 1 series, prominently ligulate; fertile achenes fusiform, with a short, slightly constricted neck, papillate only on the neck; leaves narrowly oblanceolate with shallowly sinuate to retrorsely dentate margins; Oaxaca and Puebla ..... **Chaptalia pringlei**

3. Pistillate florets in 2 series, those of the outer series ligulate, those of the outer series with ligules absent or greatly reduced; fertile achenes fusiform, without a neck or beak, sparsely papillate over the whole surface; leaves dissected into 5–7 pairs of somewhat retrorse lobules, these increasing in size distally; Querétaro ..... **Chaptalia mexicana**

2. Scapes ebracteate; achenes with a relatively long, prominently constricted neck.

4. Leaves oblanceolate-spatulate with a narrowly attenuate petiolar region; fertile achenes 6–9 mm long, including the slender neck 1/3–1/2 as long as the achene, sparsely papillate over the whole surface; northeastern Mexico ..... **Chaptalia madrensis**

4. Leaves narrowly elliptic to elliptic-obovate, without a petiolar region; fertile achenes 3.5–5.2 mm long, including the slender neck 1/4–1/5 as long as the achene, glabrous except for the sparsely papillate neck; southeastern USA ..... **Chaptalia tomentosa**

1. Leaves basally cordate; plants rhizomatous, colonial.

5. Scapes bracteate from near base to apex, bracts 6–9, linear-lanceolate, 3–5.2 mm long ..... **Chaptalia hidalgoensis**

5. Scapes ebracteate or with 1–3 small, linear bracts near the head.

6. Leaf blades thin-herbaceous, (3–)4–8 cm long, usually whitish beneath, petioles often short-winged, rarely with lyratiform extensions below the blade base; phyllaries strongly graduated in length; ray flowers 14–20 ..... **Chaptalia hintonii**

6. Leaf blades thick-coriaceous, 4.5–6.5 cm long, whitish or tawny beneath, petioles bare or with lyratiform extensions below the blade base; phyllaries strongly graduated or even in length; ray flowers 12–25 or 22–28.

7. Scapes 4–20 cm tall; leaves whitish beneath; involucres 8–15 mm wide; phyllaries strongly graduated in length; ligulate flowers 12–25 ..... **Chaptalia lyratifolia**

7. Scapes 10–20 cm tall; leaves tawny beneath; involucres 14–18 mm wide; phyllaries strongly graduated or even in length; ligulate flowers 22–28.

8. Phyllaries strongly graduated in length; ligulate flowers with corollas 12.5–19 mm long, ligules 1.3–2 mm wide, white with a purple midstripe abaxially; achenes 4–4.5 mm long ..... **Chaptalia estribensis**

8. Phyllaries even in length; ligulate flowers with corollas 9.5–12.5 mm long, ligules 0.8–1.3 mm wide, white, without an abaxial midstripe; achenes 2–2.5 mm long ..... **Chaptalia exazurea**

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DISTRIBUTION RECORDS FOR *ERYTHRANTHE* (PHRYMACEAE) IN WYOMING, MONTANA, AND UTAH

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ABSTRACT

The presence of *Erythranthe tilingii* in Wyoming is documented here for the first time. It has been collected in the southwestern Absaroka Range at closely adjacent localities in Park and Teton counties. Additional records for *E. arvensis* in Montana and Wyoming, at the eastern periphery of its range, are provided. New records for *E. microphylla* and *E. nasuta* in Utah are documented and mapped.

Erythranthe tilingii (Regel) Nesom occurs widely through the western USA at relatively high elevations (Nesom 2012, 2013). Floristic collections by Neil Snow (Snow 1989; Snow et al. 1990) in the southwestern Absaroka Range extend its range to the northeast and into the state of Wyoming (Fig. 2).

Wyoming. Park Co.: Southwestern Absarokas, ca. 45 air mi SW of Cody, along North Fork Butte Creek, W of Thorofare Buttes, T48N R108W S8,9, streamside, 8900 ft, 30 Jul 1988, *Snow 4206* (RM, Fig. 3). Teton Co.: Southwestern Absarokas, ca. 16 air mi NE of Moran, ca. 10 air mi N of Enos Lake, T48N, R112W S11, along creek, 8200 ft, 7 Aug 1987, *Snow 1831* (RM, Fig. 1).

Figure 1. *Erythranthe tilingii* from Teton Co., Wyoming, *Snow 1831*.

Figure 3. *Erythranthe tilingii* from Park Co., Wyoming, *Snow 4206*.

Erythranthe arvensis (Greene) Nesom is an annual with small, cleistogamous flowers. Occurrences in Montana and Wyoming are at the northeastern extremity of its range.

Montana. Lewis & Clark Co.: Vic. of Helena, [no date], *Kelsey s.n.* (PH). Meagher Co.: Lewis & Clark Natl Forest, Castle Mtns, Forest Rd 8905, between Cooper and Whetstone creeks, ca. 1/4 mi W of jct with Forest Rd 694, occasional wet depressions in *Pinus ponderosa* woodland, 1602 m, 23 Jun 2009, *McNeill 5074* (RM). **Wyoming**. Fremont Co.: Wind River Range, Fitzpatrick Wilderness Area, Shoshone Natl Forest, ca. 7.5 air mi SSE of Dubois, pack trail leading to Bomber Basin, spruce/fir/pine forest with granitic rocky outcrop, 7800-8600 ft, 28 Jul 1997, *Rosenthal 3094* (RM). Lincoln Co.: supporting data misplaced. Sublette Co.: Gros Ventre area, ca. 6 air mi SE of Bondurant, Fisherman Lake Creek Rd, 0.7 air mi NE of US Hwy 191, gravel pile area, 6800 ft, 16 Jul 1995, *Hartman 52244* (RM).

Figure 4. *Erythranthe arvensis* from Sublette Co., Wyoming, *Hartman 52244*.

Phrymaceae MONTANA, U.S.A.

***Mimulus guttatus* DC.**

MEAGHER COUNTY

Lewis and Clark National Forest: Castle Mountains: Forest Road 8905, between Cooper and Whetstone creeks, ca 1/4 mi W of junction with Forest Road 694.

T9N R10E S22
46.5278° N, 110.4621° W; NAD 83, GPS reading

Open meadow/ Pinus ponderosa woodland on ridgetop, running north to south; 0-15% slope; occasional wet depressions.

23 Jun 2009 Elev. 1,602 m.

Rick McNeill 5074

Floristic Inventory of Lewis & Clark National Forest and Vicinity
ROCKY MOUNTAIN HERBARIUM (RM), University of Wyoming

Figure 5. *Erythranthe arvensis* from Meagher Co., Montana, *McNeill 5074*.

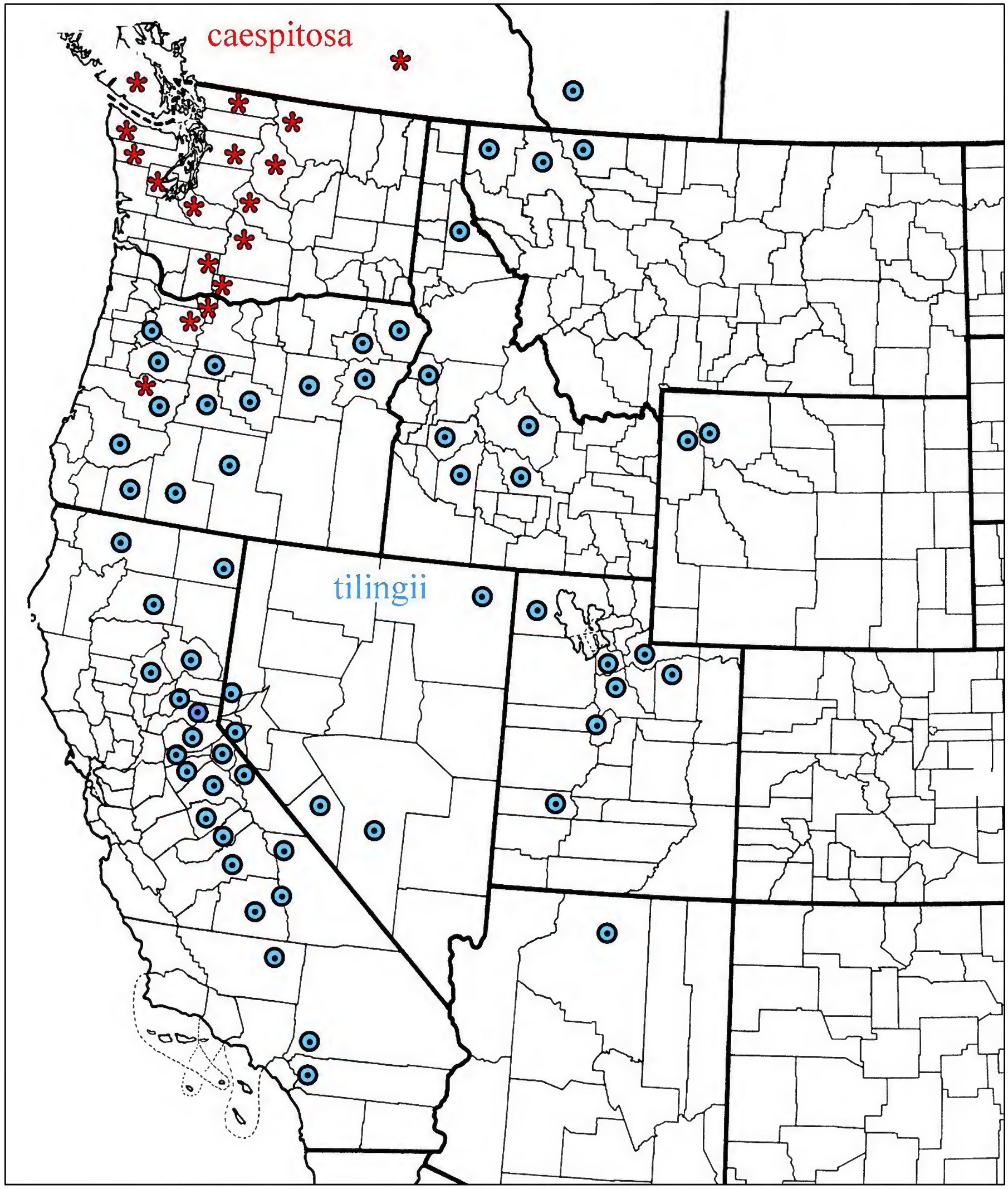

Figure 6. Distribution of *Erythranthe tilingii* and the closely related *E. caespitosa*. New records for *E. tilingii* in Wyoming are documented here.

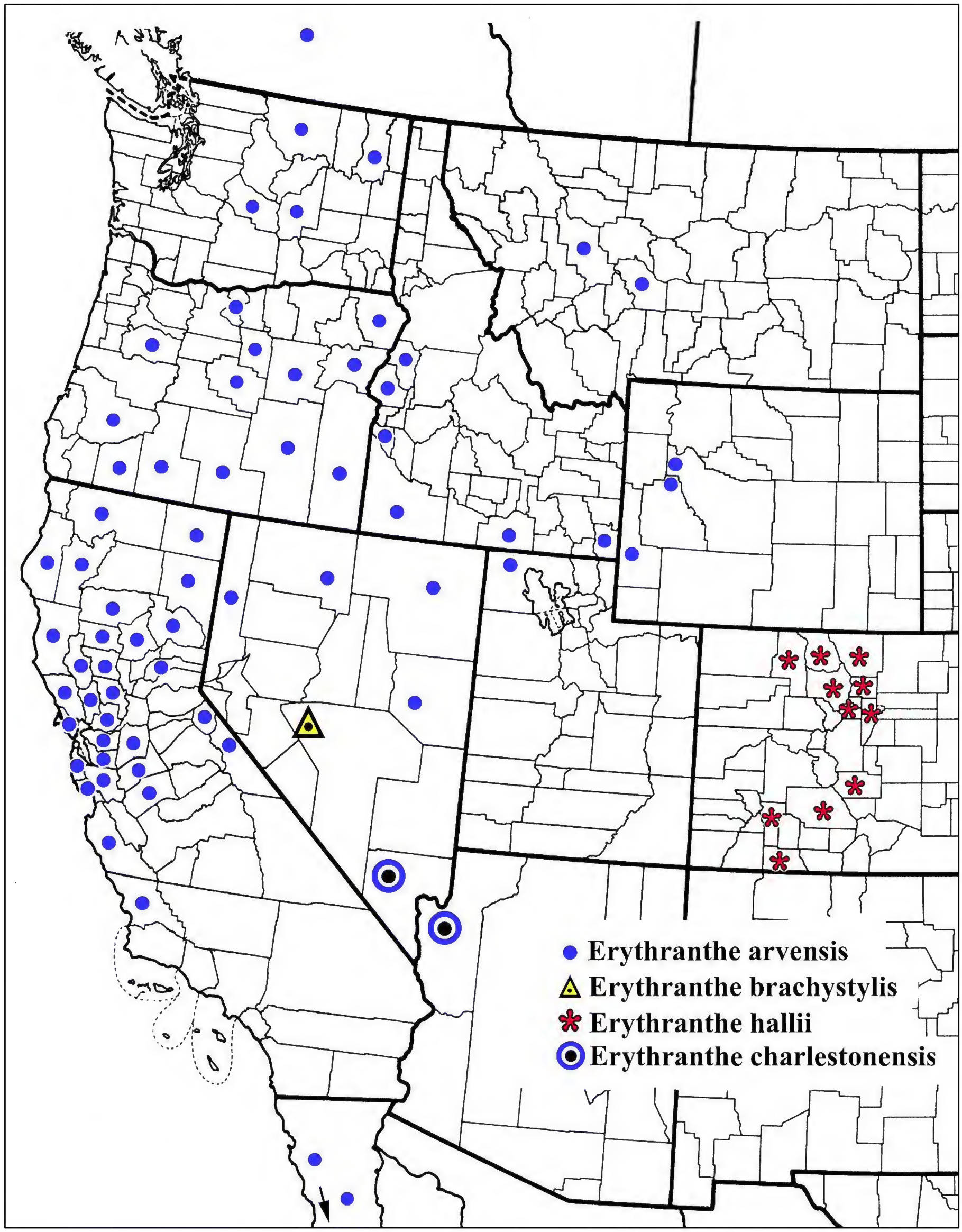

Figure 7. Distribution of *Erythranthe arvensis* and closely related species. Additional records for Montana and Wyoming are provided here.

Erythranthe microphylla and **E. nasuta**

Both of these species are wide-ranging. New records extend or confirm their occurrence in Utah.

Erythranthe microphylla. **Utah**. Cache Co.: near Tony Grove Lake, upper drainage in cirque area, streambank, 8200 ft, 18 Jul 1975, *Beedlow s.n.* (UTC image); turnoff to Tony Lake 4.1 mi from main road, rich wet soil very near stream, 9 Jul 1972, *Drake 104* (UTC image); Bear River Range, Tony Grove Lake, N end of lake in moist flats in the draw-down area exposed for at least 2 years during repairs to the dam, 8050 ft, common in moist soil, 27 Jul 2006, *Holmgren 15450* (UTC image).

Erythranthe nasuta. **Utah**. Box Elder Co.: Raft River Mts, head of Middle Fork, Dunn Canyon, most loam soil in rocks, 9000 ft, 31 Jul 1943, *Holmgren & Maguire 22196* (UTC image).

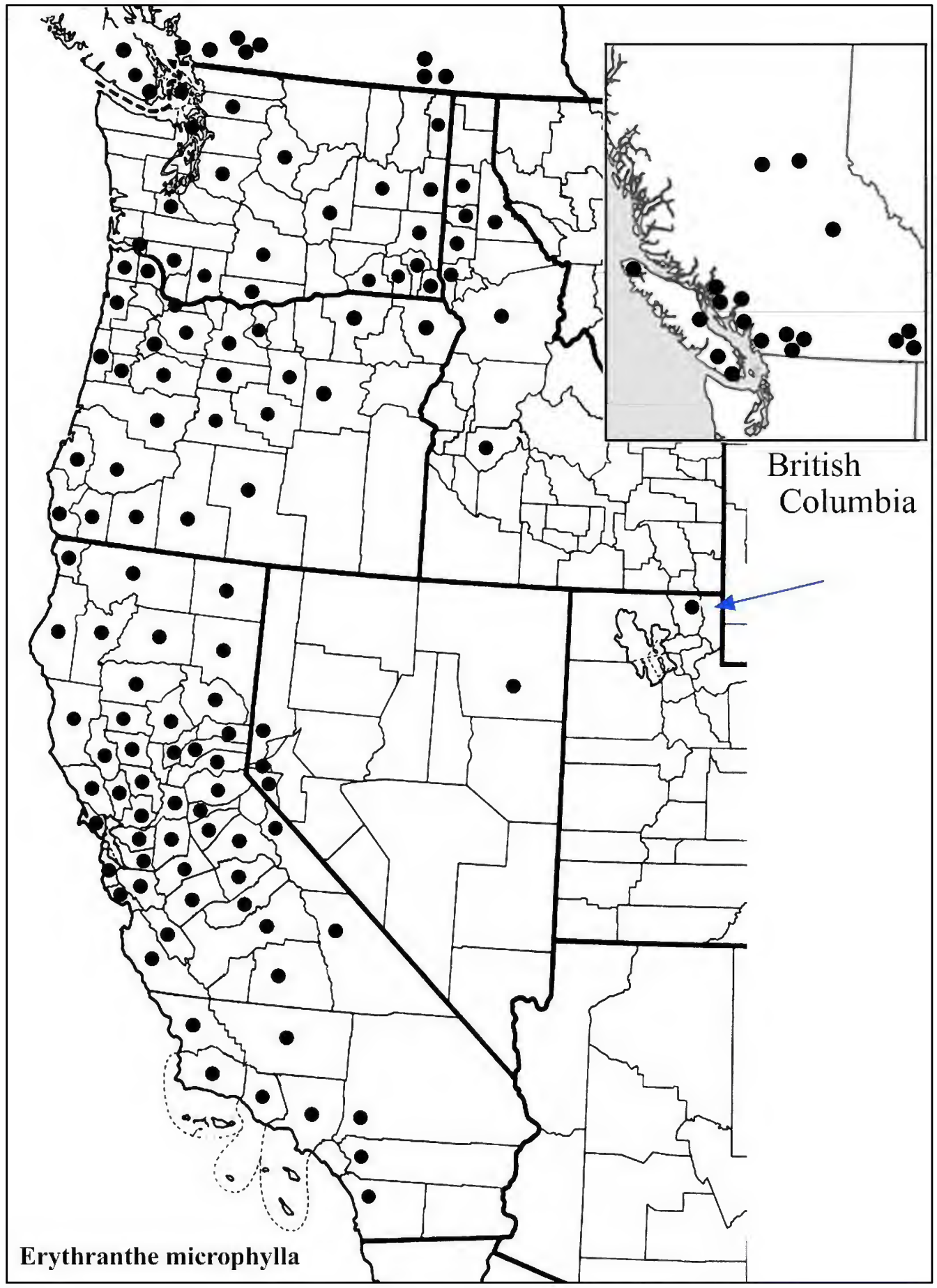

Figure 8. Distribution of *Erythranthe microphylla*. New record for Utah (Cache Co.) is documented in the text.

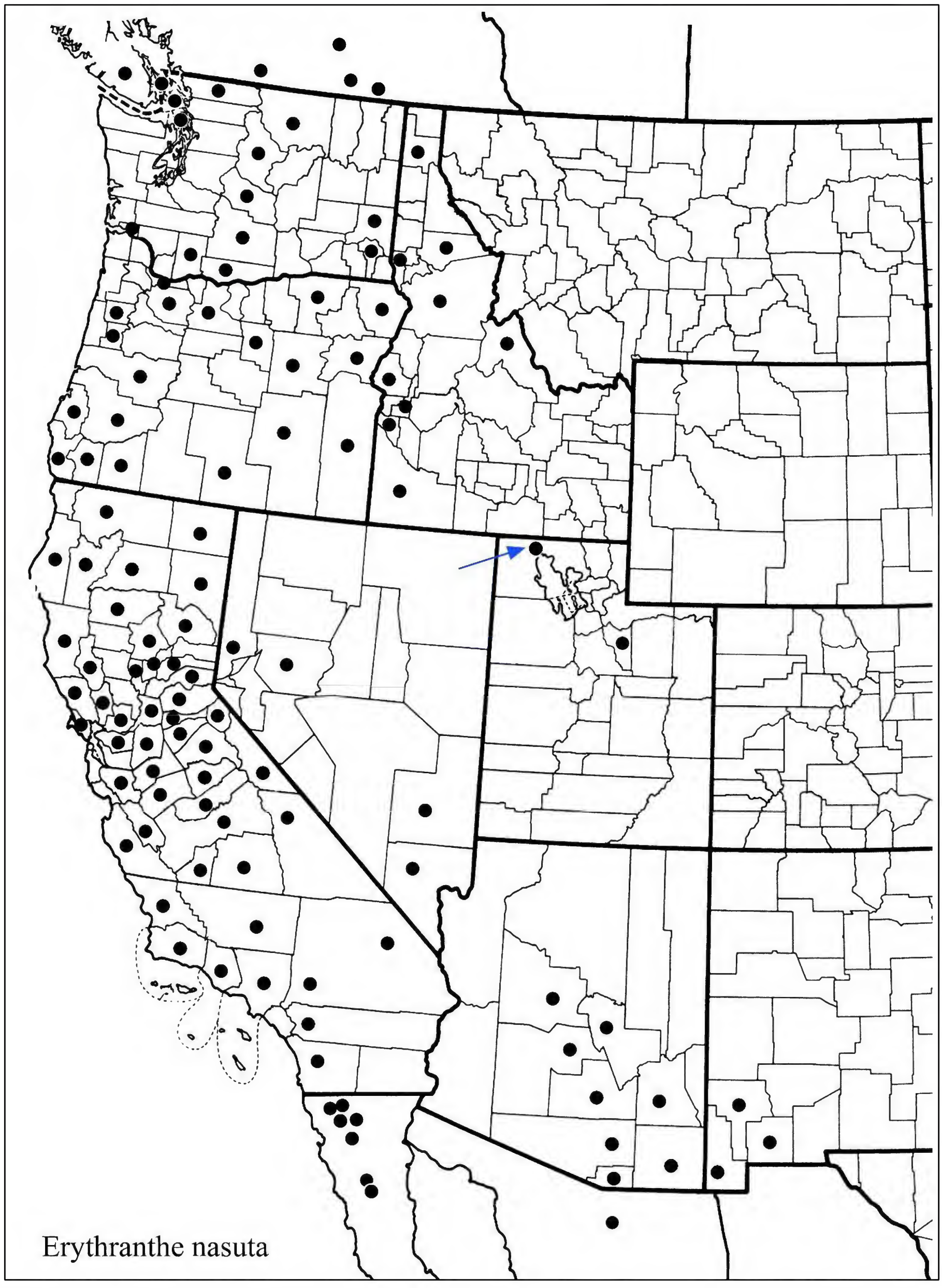

Figure 8. Distribution of *Erythranthe nasuta*. New record for Box Elder Co., Utah, is documented in the text.

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UPDATE 2019: CLASSIFICATION AND HYPOTHETICAL PHYLOGENY OF *ERYTHRANTHE* SECT. *SIMIOLUS* (PHRYMACEAE)

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ABSTRACT

An informal classification and phylogenetic diagram of the species of *Erythranthe* sect. *Simiolus* is updated, with revisions in the Guttata group, especially emphasizing new information on the presence/absence of the inverted DIV1 sequence on chromosome 8. The perennial, rhizomatous habit is hypothesized to have arisen only once in the Guttata group, with one exception. The rhizomatous clade includes the sister pair *E. tilingii* and *E. caespitosus* and a sister clade characterized by the inverted DIV1 sequence, including *E. guttata*, *E. grandis*, *E. corallina*, and *E. decora* (and its hypothesized sister, *E. scouleri*). *Erythranthe glaucescens*, which is predominantly non-rhizomatous but includes rhizomatous populations, is hypothesized to be primitively non-rhizomatous and most closely related to the annuals *E. nudata*, *E. percaulis*, and *E. filicifolia*. The remaining species of the section are annuals and are known or hypothesized to have the non-inverted DIV1 sequence. Plants previously identified as *Erythranthe arenicola* (Pennell) Nesom are considered here to be depauperate individuals of *E. grandis*.

An infrasectional classification of sect. *Simiolus* is outlined here (modified from earlier ones: Nesom 2012, 2014b), based primarily on presence/absence of the inverted DIV1 sequence, chromosome number, morphological similarity, and geography. An accompanying phylogenetic diagram also is updated (previous ones in Nesom 2013, 2014b, 2014c). The phylogenetic diagram provides a visualization of the classification and incorporates characters hypothesized to show evolutionary polarity.

Discovery by Lowry and Willis (2010) of an inversion sequence on chromosome 8 (the DIV1 inversion) in species of the *Erythranthe guttata* group has provided a significant character toward understanding phylogenetic relationships among the species of the Guttata group of *Erythranthe* sect. *Simiolus*. Further studies have revealed the sequence orientation in additional species. Major observations are these:

a. The DIV1 inversion sequence in *E. guttata* and *E. grandis* is in reverse order from that of *E. microphylla* and *E. nasuta* (Lowry & Willis 2010).

b. The *guttata/grandis* DIV1 sequence also occurs in *E. decora* (Coughlan & Willis 2018) (and can be inferred to occur in its putative sister *E. scouleri*) and in *E. corallina* (Peterson et al. 2015), which shares the UV bulls-eye floral pattern with other perennials of the *E. guttata* group as well as their rhizomatous habit, flowering phenology, and constantly moist or wet habitat.

c. The *microphylla/nasuta* DIV1 sequence occurs in *E. tilingii* (Oneal et al. 2016; Garner et al. 2016) and in *E. nudata*, *E. laciniata*, and *E. glaucescens* (Coughlan & Willis 2018). It is possible to infer, at least as a reasonable hypothesis, from O'Neal et al. (2014 — from patterns of clustering patterns of microsatellite markers in the DIV1 inversion region) that it also occurs in *E. arvensis* and *E. pardalis*. The authors noted in caution (p. 2855) that "we currently have no direct evidence of the orientation of the inversion in the larger sample of the populations that we sampled here."

Rhizome production and associated perennial duration in sect. *Simiolus* are hypothesized to be specialized (Nesom 2012–p. 9, 2014b–p. 4, 2014c–pp. 3–4; also comments below regarding *E.*

glaucescens) — non-rhizomatous annuals are the prevalent life form in species regarded as most closely related to sect. *Simiolus*, and the developmental origin of rhizomes is simple. Earlier (Nesom 2014b), I suggested that rhizomes perhaps arose independently in *E. guttata*, *E. corallina*, and *E. tilingii*, but data reviewed here support the hypothesis of a single origin of the rhizomatous habit.

Coughlan & Willis (2018, p. 1344) have tentatively agreed with this assessment of polarity. "In perennials, diversity is much lower than in annuals inside of the inversion, although measurements of diversity throughout the rest of the genome [are] relatively similar between these ecotypes (Twyford & Friedman, 2015), in line with the hypothesis that the perennial orientation of the inversion is derived and experienced a relatively old selective sweep."

In this phylogenetic hypothesis (Fig. 1), the rhizomatous, perennial habit has arisen twice in the Guttata group: (a) In the *Erythranthe guttata* sensu stricto clade, where all species are rhizomatous — here the inverted DIV1 sequence characterizes the species group sister to *E. tilingii*/*caespitosa*. Annual *E. thermalis* is hypothesized to be secondarily derived from a perennial. (b) In *E. glaucescens*, independently, which is primarily annual but has rhizomatous populations at the western periphery of its range (see further comments below).

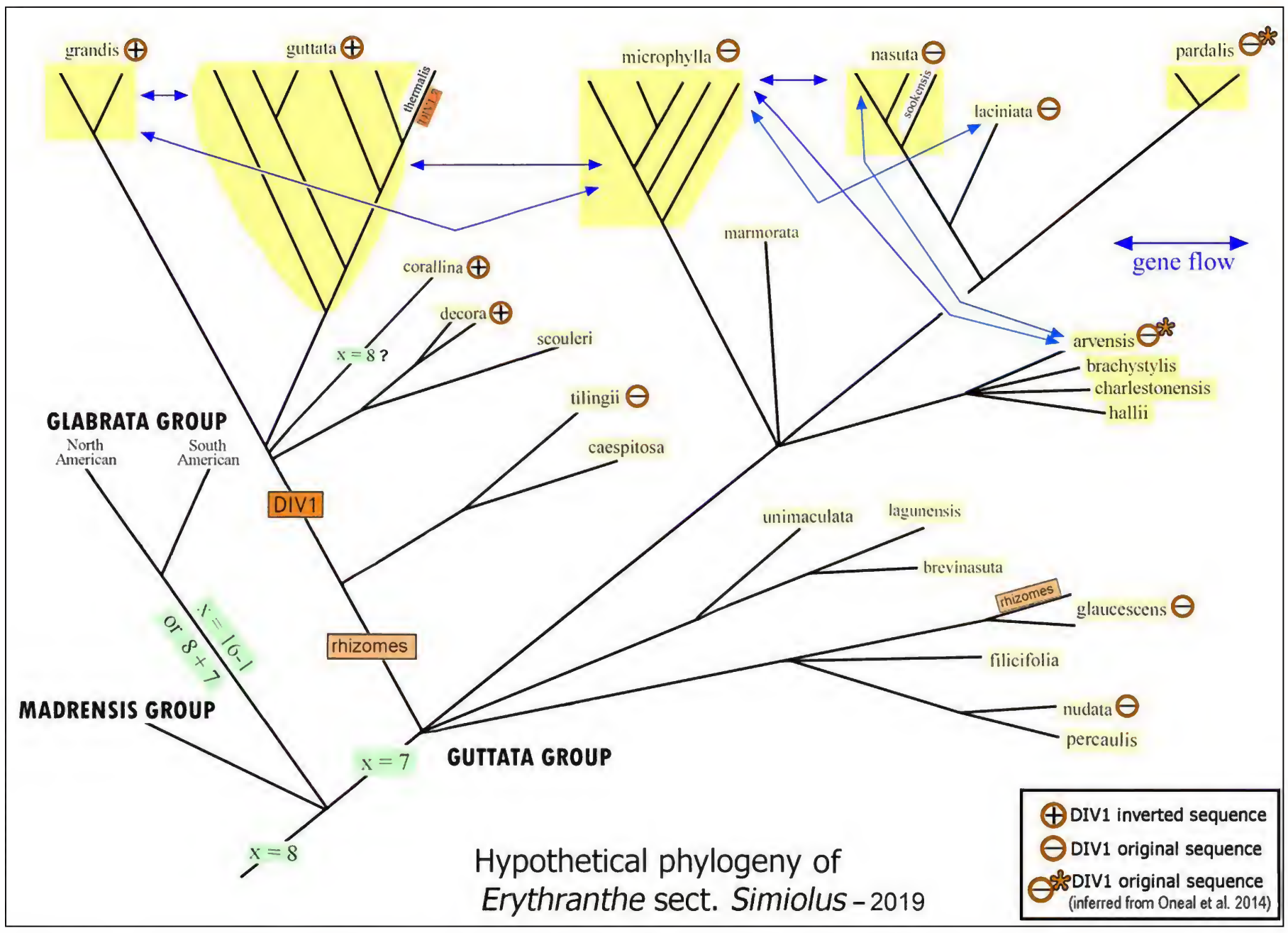

Figure 1. Hypothetical phylogeny of *Erythranthe* sect. *Simiolus*. The 50 species are divided into 3 main groups: **Madrensis** (base chromosome number, x = 8), **Glabrata** (x =15), and **Guttata** (x = 7). Taxa of the Guttata group are highlighted in yellow. Gene flow is inferred from morphological patterns. Extra branches within *E. decora*, *E. grandis*, *E. guttata*, *E. microphylla*, *E. nasuta*, and *E. pardalis* indicate the existence of regional morphological and/or cytological variants.

Informal infrasectional classification of sect. *Simiolus*

Plants are allogamous and perennial unless otherwise noted: * = autogamous; ^{A} = annual duration.

1. **Madrensis group**

Subgroup A (*E. madrensis*, *E. pallens*, *E. calciphila**^{A}, *E. pennellii*, *E. visibilis**^{A}). Perennial or annual; calyces 5-lobed or mostly 3-lobed; flowers small (allogamous or autogamous); western Mexico into southwestern USA. Base chromosome number x = 16 (or 8).

Subgroup B (*E. chinatiensis**, *E. dentiloba*, *E. diminuens**, *E. parvula**). Perennial, mat-forming; calyces 5-lobed or with tendency toward 3-lobed; flowers relatively small, allogamous or autogamous; corolla lobes laciniate to fimbriate; southwestern USA and northwestern Mexico. Base chromosome number x = 16 (or 8).

2. **Glabrata group**

Subgroup A - North American (*E. michiganensis*, *E. geyeri**, *E. inamoena**, *E. cordata**^{A}, *E. regni**^{A}, *E. utahensis*). Perennial and annual, rhizomatous or rooting at proximal nodes, annual and without rhizomes in *E. regni*; calyces not closing; flowers small and autogamous or (*E. michiganensis*) larger, chasmogamous and allogamous; central USA, Mexico. Base chromosome number x = 15

Subgroup B - South American (*E. acaulis*, *E. andicola, E. cuprea*, *E. depressa*, *E. glabrata*, *E. lacerata*, *E. lutea*, *E. naiandina*, *E. parviflora*, *E. pilosiuscula*, and perhaps others). Perennial and annual, rhizomatous or rooting at proximal nodes; calyces not closing; flowers chasmogamous and allogamous; South America (*E. glabrata* ranges into North America). Base chromosome number x = 15.

3. **Guttata group**

Subgroup A, the Guttata subgroup. Perennial and annual; leaves oblong or elliptic to obovate, margins remotely or closely toothed; flowers relatively large and chasmogamous and allogamous; western USA and northwestern Mexico. Base chromosome number = 14 (7) for *E. guttata*, *E. grandis*, *E. decora*, and *E. tilingii*.

Reports for *E. corallina* are $2n$ = 48 and 56, perhaps based on x = 8; these need to be restudied/confirmed, particularly the count of $2n$ = 48.

Series 1 (*E. grandis*, *E. guttata*, *E. thermalis**^{A}, *E. corallina*). It is hypothesized that the annual *E. thermalis* is derived from perennial *E. guttata* (see commentary and references in Nesom 2012, p. 44–45) and is thus predicted to have the DIV1 inversion of its progenitor. Plants previously identified as *Erythranthe arenicola* (Pennell) Nesom are considered here to be within the range of variation of *E. grandis* (see comments below).

Molecular studies continue to assert/assume that "Mimulus guttatus" (without specifying whether the annual or perennial form) is the progenitor of the "species complex" (without specifying what is meant by that phrase) (e.g., Ferris et al. 2015; Ferris & Willis 2018). Figure 1 above indicates why this view is problematic (and see Nesom 2013–p. 4–5 and 2014b–p. 4 for discussion).

Series 2 (*E. decora*, *E. scouleri*). Perennial; flowers large; rhizomes numerous; leaf margins closely and regularly toothed; styles densely hairy; Washington and Oregon. Base chromosome number x = 7. Coughlan et al. (2018, Fig. 1) found that diploids and tetraploids occur within *E. decora* (diploids southern, tetraploids mostly northern) and that two geographic clades exist among the diploids. Strong post-zygotic reproductive barriers exist between the northern and southern diploids and between each of these and the tetraploids. The three races are indistinguishable in morphology.

Erythranthe scouleri is hypothesized to share the inverted DIV1 sequence with *E. decora*, in view of their morphological and geographical coherence, suggesting immediate common ancestry. Field studies by Lomer (2019) have contributed to an understanding of the morphology, geography, and ecology of *E. scouleri*.

Subgroup B, the Tilingii subgroup (*E. tilingii*, *E. caespitosa*). Perennial; flowers large, chasmogamous and allogamous; filiform rhizomes profusely produced; mostly high elevation; western USA (see range extension in Nesom 2019a). Base chromosome number x = 14 (7) (*E. tilingii*: $2n$ = 28, 56).

In a STRUCTURE analysis of noninversion microsatellite markers (Oneal et al. 2014, Fig. 1), *E. tilingii* clusters (K2) with samples of *E. guttata* from Colorado and Washington and some in Oregon. For the markers in the inverted sequence (Fig. 2), *E. tilingii* unambiguously appears to cluster (K2 and K3) with the other perennials, although Oneal et al. noted (p. 2851) that "it is difficult to tell whether [*E.*] *tilingii* clusters more with the annuals or the perennials for the inverted markers, however, as it appears to harbour variation segregating within both."

The placement here of *E. tilingii* at the base of the clade with other perennials reflects the interpretation of rhizomes as specialized and (parsimoniously) their origin in the clade's ancestor. Alternatively, as in *E. glaucescens*, it is not implausible that rhizomes evolved independently in *E. tilingii*/*caespitosus*.

Earlier (Nesom 2014b), I placed "E. minor" in the *E. tilingii* group, but further study shows that plants identified as that species are best considered within the widespread and variable, perennial *E. guttata*, and *E. minor* is now treated as a synonym of it (Nesom 2019b).

Subgroup C, the Unimaculata subgroup (*E. unimaculata*[A], *E. lagunensis*[A], *E. brevinasuta**[A]). Annual; sw USA and nw Mexico (*E. unimaculata*) and Baja California Sur (*E. lagunensis*, *E. brevinasuta*). *E. unimaculata* and *E. lagunensis* have large corollas and are morphologically similar to *E. guttata* in many features but are annuals, without rhizomes. *E. brevinasuta* has small flowers (cleistogamous, autogamous) but produces denticulate calyx margins, an unusual character shared with *E. lagunensis*, and it is hypothesized that the latter two are sister species. The corolla palate of *E. unimaculata* dries a distinctive blue-green — the UV pattern almost certainly is 'runway' (sensu Peterson et al. 2015), implying that it has the non-inverted DIV1 sequence.

Subgroup D, the Microphylla subgroup (*E. microphylla*[A], *E. marmorata*[A]). Annual; flowers large or variable in size, chasmogamous and allogamous; basal and proximal cauline leaves often purplish on one or both surfaces; central California (*E. marmorata*) and more broadly distributed (*E. microphylla*). Base chromosome number x = 14 (7).

Subgroup E, the Nasuta subgroup (*E. nasuta**[A], *E. laciniata**[A], *E. pardalis**[A]). Annual; flowers small (cleistogamous or slightly open, autogamous; basal and proximal cauline leaves often purplish (*E. nasuta*, *E. laciniata*); flowers often produced at all nodes, proximal to distal; Sierra Nevada of USA (*E. laciniata*, *E. pardalis*) and more broadly distributed (*E. nasuta*). Base chromosome number x = 14 (7).

Subgroup F, the Arvensis subgroup (*E. arvensis**[A], *E. brachystylis**[A], *E. charlestonensis**[A], *E. hallii*[A]). Annual, sometimes rooting at lower nodes (*E. arvensis*) but not rhizomatous; flowers often cleistogamous, all autogamous, produced from distal nodes; western USA. Base chromosome number x = 14 (7); *E. hallii* is reported as n = 16. The Arvensis subgroup might reasonably considered a single variable and widespread species (*E. arvensis*) with several peripheral isolates.

Subgroup G, the Nudata subgroup (*E. nudata*[A], *E. percaulis*[A], *E. filicifolia*[A], E. *glaucescens*[A]). Annual; leaf blades of reduced surface area; flowers produced mostly from distal nodes, small and autogamous in *E. filicifolia* and *E. percaulis*; narrow endemics of north-central California, hypothesized here to represent a single clade, emphasizing their geographic coherence. Base chromosome number unknown. *E. nudata* and *E. percaulis* probably are sister species; *E. percaulis* has smaller cauline leaves and distinctly smaller, autogamous flowers. *E. filicifolia* and *E. glaucescens* each have distinctive leaf morphology.

The newly described *Erythranthe filicifolia* was hypothesized (Nesom 2013a, 2014a, 2014b) to be most closely related to *E. nudata* and *E. percaulis*. Ferris and Willis (2018) found a strong hybrid sterility barrier between *E. filicifolia* and both *E. guttata* and *E. laciniata* and that *E. filicifolia* is more genetically distant from *E. laciniata* than from *E. guttata* and *E. nasuta* — concluding that *E. filicifolia* may have arisen from an ancestor other than the "wide-ranging *M[imulus] guttatus*," offering no contradiction to the hypothesis of relationship summarized here. Oneal et al. (2016) characterized the hybrid seed inviability that underlies reproductive isolation between *E. nudata* and *E. microphylla*.

Plants in most populations of *Erythranthe glaucescens* are annual but those of at least two populations in Butte County (ca. 7 miles apart) are rhizomatous (Nesom 2012, p. 61; Taylor 2013). If the species were interpreted as primitively rhizomatous, it would be placed here as a 3rd subgroup in the

'guttata' sensu stricto clade (following the parsimonious view that rhizomes have arisen only once in the Guttata group), but the tentative interpretation here is that the rhizomatous populations of *E. glaucescens* have arisen (probably in a single event) from a conspecific, non-rhizomatous one.

Erythranthe arenicola* is a synonym of *E. grandis

I recognized at specific rank (Nesom 2012) depauperate, small-flowered plants from sandy, seaside habitats in Monterey Co., California, originally described by Pennell (1947) as *Mimulus guttatus* subsp. *arenicola*. I interpreted their duration as annual and hypothesized that they were evolutionarily derived from stoloniferous *Erythranthe grandis*. After studying a set of collections at PH from the same area, it now seems clear that they also are stoloniferous and range in sizes typical of *E. grandis* down to depauperate individuals (stems 6–15 cm tall, calyces 10–12 mm long) similar to those originally named by Pennell. All are encompassed within the range of variability of *E. grandis*.

Similarly, another "beach form" described in the same publication by Pennell as *Mimulus guttatus* subsp. *litoralis* is a variant of *Erythranthe grandis*. These include plants from seaside habitats in northern California and Oregon, with prostrate or decumbent-ascending stems that often root at the nodes. They have been collected from cliffs and bluffs, wet banks, and dunes.

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TAXONOMIC STATUS OF *ERYTHRANTHE MINOR* (PHRYMACEAE)

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ABSTRACT

Most plants in Colorado previously identified as *Erythranthe guttata*, *E. tilingii*, and *E. minor* apparently represent a single entity, here identified within *E. guttata* sensu stricto as the "minor morph," characterized especially by densely hirtellous, eglandular vestiture. *Erythranthe guttata* with glandular vestiture is known from Moffat County and in several north-central counties. The minor morph occurs northward into Albany and Carbon cos., Wyoming, southward into northern New Mexico, and slightly westward into Utah. It appears to be relatively sharply delimited in morphology from glandular *E. guttata* to the south and southwest, but plants closely similar to the minor morph extend northwestward to the Pacific coast and make its recognition as a species distinct from *E. guttata* problematic.

In earlier treatments (Nesom 2012; Nesom & Fraga 2019), *Erythranthe minor* (A. Nels.) Nesom has been recognized as a species perhaps closely related to *E. tilingii* (Regel) Nesom but distinct in morphology and nearly endemic to Colorado. After opportunities to examine a larger number of collections, evidence suggests that it is better identified as part of the widespread and variable *E. guttata*.

In the protologue of *Mimulus minor*, Nelson (1904) contrasted it with *M. guttatus*, pointing out the smaller corollas in the new species. Pennell (1951) treated *Mimulus minor* as a distinct species occurring from Oregon and Idaho south to Utah and New Mexico — he also emphasized the short corollas and noted that the pedicels produced only eglandular hairs. In 2012 I saw similarity in the Colorado plants to *Erythranthe tilingii* in their relatively high elevation habitat (subalpine to alpine, 8000–12,100 feet, rarely down to 7000 feet) and their filiform, prolifically produced rhizomes that often arise from lower cauline nodes, identifying them as *Erythranthe minor* and contrasting them with *E. tilingii* by their shorter corolla tube-throats (9–11 mm vs 15–25 mm) only slightly exserted beyond the calyx margin (but apparently herkogamous and allogamous) as well as their distinctive geographic range.

The Colorado plants are distinctive and consistent in vestiture and corolla morphology, but similar morphology appears sporadically elsewhere in the range of more typical *Erythrante guttata* and a formal distinction is problematic to maintain. Almost all Colorado plants previously identified as *E. guttata*, *E. tilingii*, and *E. minor* are characterized by short corolla tubes (Figs. 1, 2, 3) and densely and minutely hirtellous, eglandular stems, peduncles, and pedicels (Fig. 4) — the range of this "minor morph" extends southward into northern New Mexico, slightly westward into Utah, and northward into Albany and Carbon cos., Wyoming (Fig. 5). To the south and southwest, there appears to be a discontinuity between the minor morph and more typical *E. guttata* with longer corolla tubes and vestiture with gland-tipped hairs, but beyond southern Wyoming these morphological features appear sporadically northwestward and with intergradation to the Pacific coast (northern Oregon, Washington, British Colombia).

In southern Oregon, California, and into Nevada and northwestern Arizona, vestiture of *Erythrante guttata* is consistently villous-glandular, usually without eglandular hairs. Elsewhere in its geographic range (except for the Colorado segment), vestiture characteristically is a mix — hirsute-hirtellous and villous-glandular — with both eglandular and glandular hairs.

Figure 1. *Erythranthe guttata* in Colorado, the “minor morph.” The minor morph usually produces a few distal flowers but variants can produce a raceme like that often seen in broadly distributed *E. guttata.*

Figure 2. *Erythranthe guttata* in Colorado, the "minor morph." Left: Groundhog Meadow Trail, Rio Grande Co.. Right: Wildcat Trail, Montezuma Co. Photos by Al Schneider, used by permission.

Figure 3. *Erythranthe guttata* in Colorado, along Wildcat Canyon Stream, Montezuma Co. Photo by Al Schneider, used by permission.

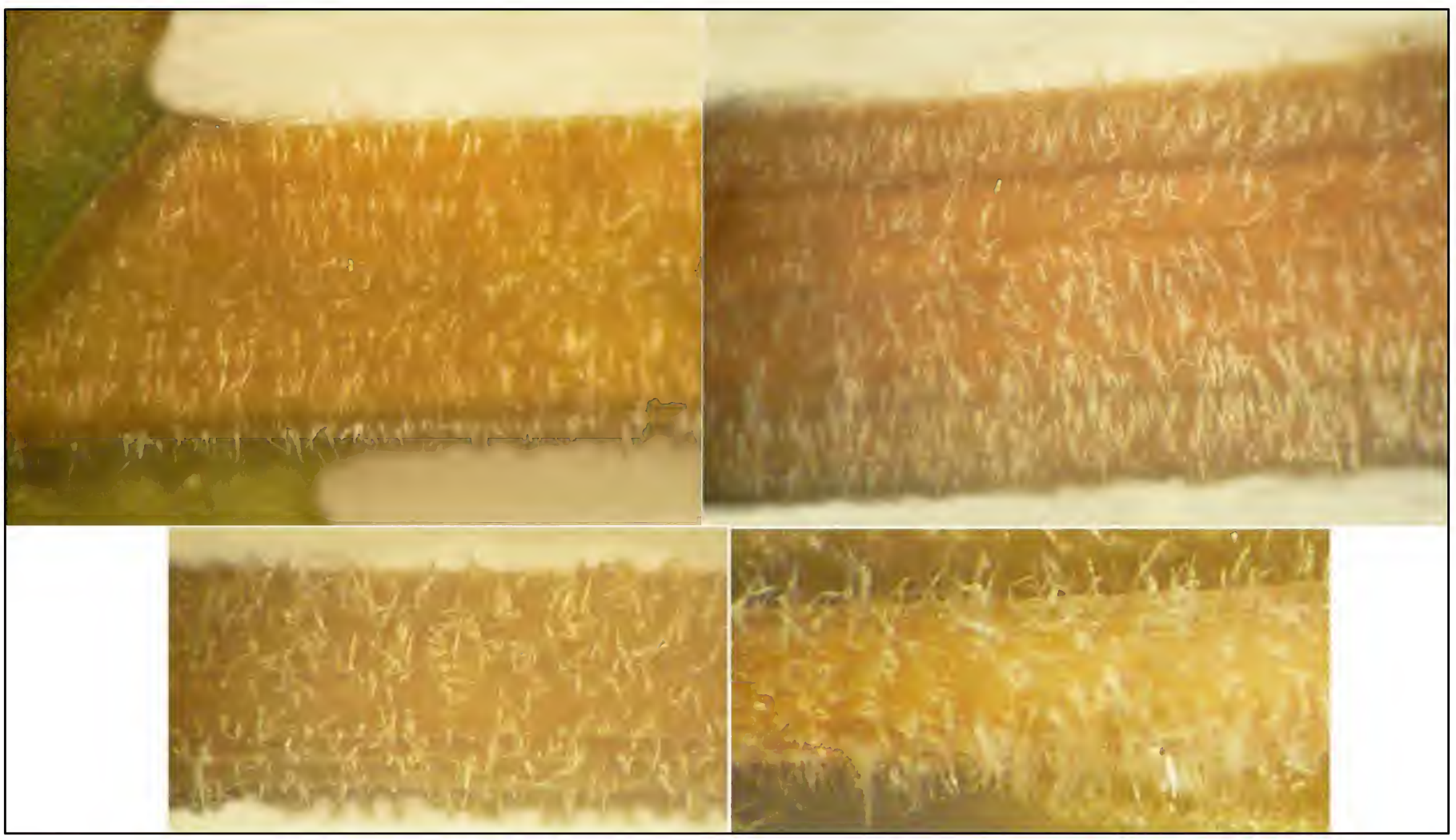

Figure 4. *Erythranthe guttata* (the "minor morph") in Colorado. Characteristic upper cauline vestiture.

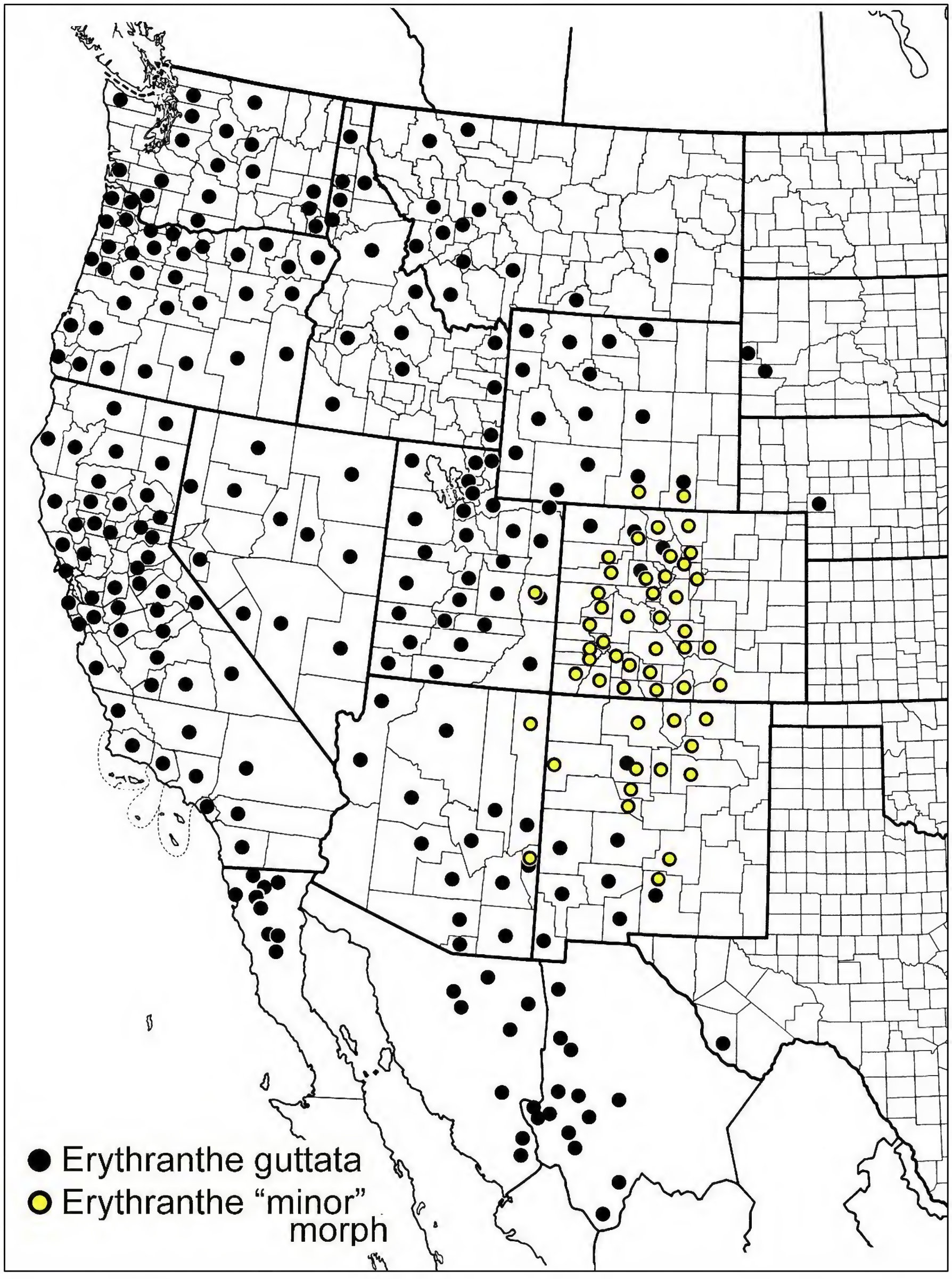

Figure 5. Distribution of *Erythranthe guttata*, including the minor morph, in the USA and Mexico. It is characterized mainly by the densely hirtellous, eglandular vestiture of at least the peduncles and pedicels. Plants similar to the minor morph continue sporadically across Wyoming to northern Oregon, Washington, and southern British Columbia. The discontinuity appears to be more sharply defined southwestward.

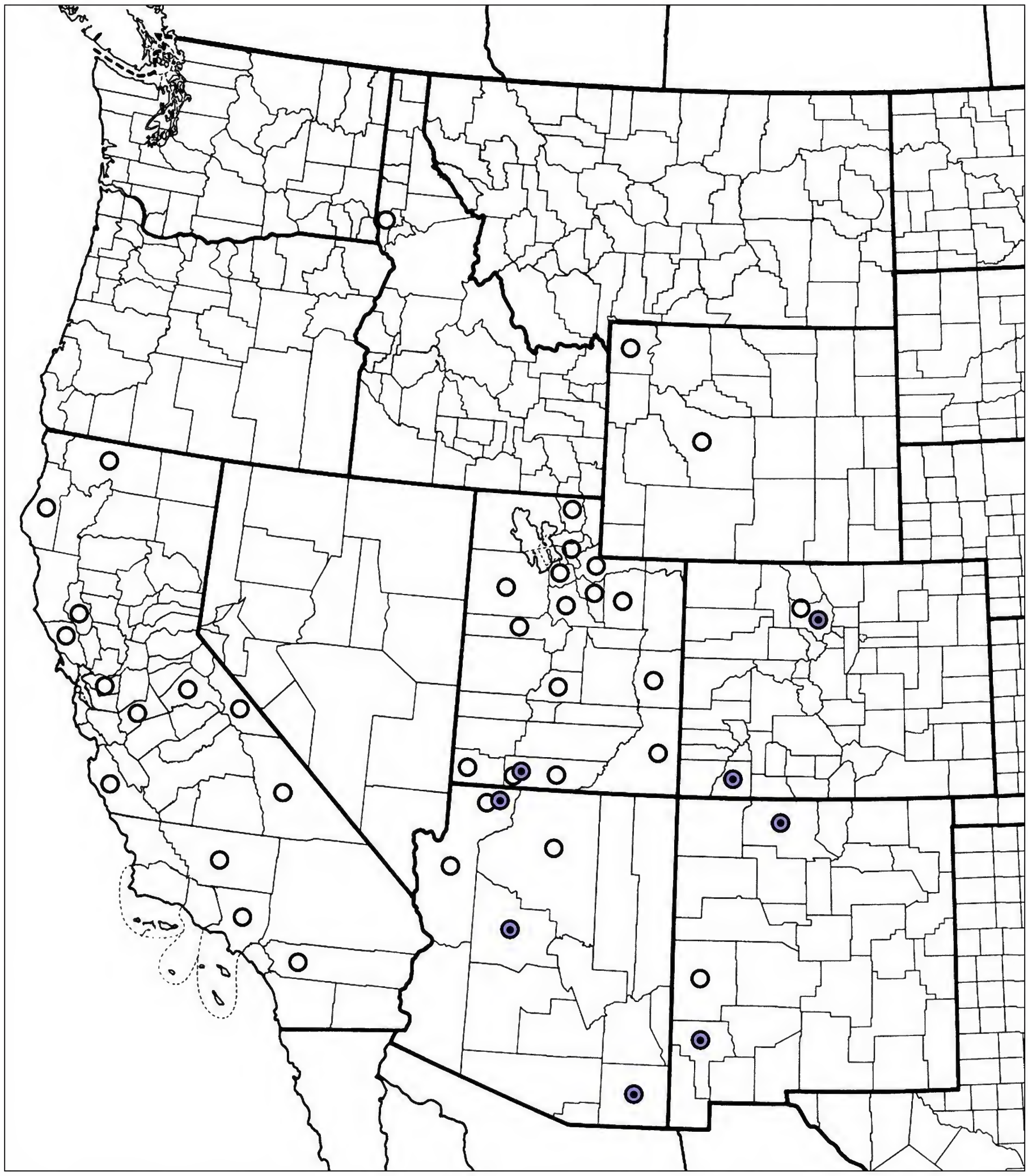

Figure 6. Chromosome counts reported for plants identified as *Mimulus guttatus*. Open circles are diploid; dotted blue circles are tetraploid. Overlapping symbols in Mohave Co. Arizona, and Kane Co., Utah, denote single populations with both ploidy levels. Tetraploids also are reported from coastal localities in British Columbia and Alaska. Originally Map 8 in Nesom (2012), which see for supporting data.

As noted earlier (Nesom 2012), the distribution of tetraploid chromosome counts for *Erythranthe guttata* (Fig. 6) seems to be largely congruent with the distribution of the minor morph. If the morph proves to be consistently tetraploid, it may be reproductively isolated from diploid *E. guttata*. More data are needed to delineate in detail the geographic boundary between diploids and tetraploids, and collections from Arizona and southeastern Utah should be reexamined for vestiture type.

In the earlier concepts of *Erythranthe minor* (Nesom 2012; Nesom & Fraga 2019) the vestiture was described as "densely minutely hirtellous and eglandular or with a mixture of hirtellous and gland-tipped hairs." As indicated by Figure 5, however, within the range of the minor morph, glandular plants are uncommon.

Documentation of sympatry of the "minor morph" and glandular-stemmed plants of *Erythranthe guttata* in Arizona, Colorado, and New Mexico.

ARIZONA.

Greenlee Co.: Hannagan Meadow area, 8900-9300 ft, 21 Jun 1962, *Schmidt 170* (ARIZ)— the minor morph. Other collections examined from Greenlee Co. are *E. guttata* with minutely glandular stems.

COLORADO.

Eagle Co.: Gore Range, ca. 12.5 mi SE of Vail, just N of Vail Pass, *Holt 2310* (RM)—vestiture small plants with solitary heads and vestiture greatly reduced, minutely hirtellous; Sawatch Range, ca. 6 air mi S of Minturn, Notch Mtn Creek, Holy Cross Wilderness, *Kirkpatrick 4181* (RM)—pedicels and calyces glandular; Sawatch Range, ca. 15 air mi S of Dowds Junction, along Missouri Creek, *Kirkpatrick 4514* (RM)—similar to *Holt 2310*. The following from Eagle Co. are typical minor morph: Sawatch Range, ca. 6 air mi S of Vail, *Holt 1713* (RM); Gore Range, ca. 5 air mi E of Vail, *Holt 3130* (RM); Gore Range, ca. 5 mi ENE of Vail, *Holt 3040* (RM); Gore Range, ca. 8 air mi E of State Bridge, *Kirkpatrick 2656* (RM).

Grand Co.: Arapaho Natl Forest, Byers Peak Wilderness, Lake Evelyn Trail, ca. 9.5 air mi WSW of Fraser, *Foley 4251* (RM)—vestiture greatly reduced, pedicels and calyx barely hirtellous, stems glabrous; Arapaho Natl Forest, Vasquez Mtns, ca. 2 air mi ESE of Byers Peak and ca. 8 air mi SW of Fraser, *Foley 7621* (RM)—distal stems, pedicels, and calyces stipitate-glandular and sparsely hirtellous. Other collections examined from Grand Co. are the "minor morph."

Routt Co.: W slope of Park Range, Rte 40, along cold brook, *Pennell & Schaeffer 22369* (PH)––nearly glabrous, with a few glands. Other collections from Routt Co. are the "minor morph."

NEW MEXICO.

Sandoval Co.: Jemez Mtns, Seven Springs Fish Hatchery, riparian on river, *Reif 441* (RM)—stems and calyx sparsely villous-glandular. Other collections examined from Sandoval Co. are the "minor morph."

Nomenclatural summaries

The two names below are typified by plants of the "minor morph."

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Mimulus puberulus Greene ex Rydb., Fl. Colorado, 311. 1906 [Greene, Leafl. Bot. Observ. Crit. 2: 4. 1909]. *Mimulus guttatus* var. *puberulus* (Greene ex Rydb.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 170. 1924. **LECTOTYPE** (Nesom 2012): **USA**. **Colorado**. [Archuleta Co.:] Pagosa Springs, 27 Jul 1899, *C.F. Baker 587* (ND-Greene 046404!; isolectotypes: F image, MO!, ND-Greene!, NY image, POM!, RM!, UC!, US image).

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TAXONOMIC NOTES ON MEXICAN *GRINDELIA* (ASTERACEAE)

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ABSTRACT

Grindelia palmeri (including G. *inuloides* var. *latamplexa* Nesom) is a distinctive species of San Luis Potosí and Querétaro — its distribution is mapped and collections cited. *Grindelia macvaughii* was described only from northeastern Jalisco, but it is documented here and mapped with additional localities from Aguascalientes, southern Zacatecas, and northeastern Michoacan. *Grindelia macvaughii* and *G. inuloides* are allopatric — the distribution of the latter also is mapped. *Grindelia subdecurrens* and *G. oxylepis* are similar but essentially allopatric in distribution — their ranges are mapped and a morphological contrast is provided.

In a taxonomic review of *Grindelia* in Mexico, clarifications from earlier observations (Nesom 1990) can be made. Observations here include *Grindelia palmeri*, *G. macvaughii*, and *G. subdecurrens*. Observations on variants of *G. inuloides* will follow in a separate account.

1. GRINDELIA PALMERI Steyerm., Ann. Missouri Bot. Gard. 21: 471. 1934. **TYPE**: **MEXICO**. **San Luis Potosí**. [Mpio. Zaragoza]: Alvarez, 28 Sep-3 Oct 1902, *E. Palmer 163* (holotype: US!; isotypes: BM image, CM image, F image, GH!, MEXU image, MO!, NY image).

Grindelia inuloides var. *latamplexa* Nesom, Phytologia 68: 327. 1990. **TYPE**: **MEXICO**. **Queretaro**. [Mpio. Pinal de Amoles]: 2.7 km SW of Pinal de Amoles on Hwy 120, 1.7 km NE of the SARH forestry fire station, 27 Dec 1980, *J.M. Canne 1941* (holotype: F!).

Perennial, from a woody, fibrous-rooted corm. **Stems** 25–80 cm tall, sometimes purplish, sparsely to moderately villous, stipitate-glandular. **Leaves** oblong or oblanceolate-oblong to ovate-lanceolate, becoming triangular-ovate distally, cauline mostly 3–5 cm long, 8–18 mm wide, somewhat to little reduced upward, often continuing to immediately below heads as foliar bracts, base auriculate-clasping, decurrent 1–3 mm, apex mostly obtuse to acute, margins with sharp-pointed, eglandular teeth, surfaces minutely hirtellous to sparsely short-pilose, stipitate-glandular to punctate-glandular, often viscid. **Involucres** 15–20 mm wide, phyllaries more or less even in length, relatively evenly herbaceous, narrowly triangular. **Achenes** apparently monomorphic; pappus awns smooth-edged.

Que, San; limestone soils in pine, pine-oak, oak, or oak-acacia woodlands, roadsides, pastures; 1520–2600 m; (Apr–)Jun–Jan.

Additional collections examined. **Querétaro**. Mpio. Pinal de Amoles: Al S de la ciudad de Pinal de Amoles, bosque latifoliado esclerofilo caducifolio, 2600 m, 24 Aug 1999, *Avlos 214* (MEXU); 2 km N del Puerto del Tejamanil, bosqjue de pino-encino en canada, 2450 m, 7 Jun 1983, *Fernandez N. 1565* (MEXU image); Pinal de Amoles, bosque de pinos, encinos, ailes y compuestas principalmente, 2000-2200 m, 19 Aug 1992, *Orozco et al. 10,081* (MEXU); 1.5 mi W of Pinal de Amoles, 11 Nov 1976, *Turner 76-13* (LL); 6.5 mi S of Pinal de Amoles along Hwy 120, 16 Jan 1977, *Urbatsch & Pridgeon 3038* (LL); aprox. 2 km al NE de Pinal de Amoles, por la carr. a Cadereyta, bosque mixto de *Pinus-Quercus*, 20 Jul 1986, *Villaseñor 940* (MEXU); Pinal de Amoles, bosque de *Pinus patula*, 2600 m, 10 Mar 1978, *Zamudio 2663* (MEXU). Mpio. San Joaquín: 8 km al E de San Joaquín, sobre camino al Ahuacate, orilla de camino, terreno de cultivo, 2400 m, 29 Nov 1992, *Fernández N. 4834* (MEXU). **San Luis Potosí**. [Mpio. Rayón?]: 5 mi W of San Francisco (33 km W of Santa Catarina) on hwy from Rio Verde to SLP, side road to microwave tower on side of hill with oaks, locally common along road and in pasture, 8100 ft, 18 Jul 1982, *Fryxell 3808* (MEXU image); microwave hill of Rte. 70 E of San Luis Potosí, W of Santa Catarina, *Loockerman*

40015 (TEX). Mpio. San Luis Potosí: Along Mex. Hwy 70 E of San Luis Potosí, crest of ridge with *Quercus* and *Buddleja* near microwave tower, 2590 m, 25 Oct 1983, *Breedlove 59337* (MEXU image). Mpio. Zaragoza: Alvarez, terreno abiertos de bosque de pino encino, 2340 m, 29 Oct 1995, *Bye 20579* (MEXU image); Sierra de Alvarez, comunidad de San Francisco, en el potrero, bosque de *Quercus*, 2044 m, 9 Sep 2003, *Colin M. 45* (MEXU image); Valle de los Fantasmas, bosque de encino, 1680 m, Apr 1992, *Gómez L. 855* (MEXU image); Sierra de Alvarez, Alvarez, oak grove on limestone, 2200-2400 m, 30-31 Jun 1934, *Pennell 17892* (PH); 33 km E of San Luis Potosí or 1 km of Puerto de la Huerta on Hwy. 86, *Roe et al. 144* (TEX).

Figure 1. *Grindelia palmeri*, CM isotype. San Luis Potosí.

Figure 2. *Grindelia palmeri*. Alvarez, San Luis Potosí, *Colin M. 45*.

Figure 3. Representative morphology of *Grindelia palmeri* in Querétaro. Left: *Fernandez 4834*. Middle: *Orozco 10081*. Right: *Villaseñor 940*.

Grindelia palmeri is similar to *G. inuloides* in its sharp-toothed leaves and tendency to produce stipitate-glandular vestiture. Leaves usually are larger in *G. palmeri* and the auriculate-clasping leaf base is diagnostic even when basal parts are not collected. No unambiguous intermediates between them have been seen. Bartolia and Tortosa (2012) cited collections from Colima and Michoacan in their concept of *G. palmeri*.

1. Perennial from a woody taproot; cauline leaves clasping at base but not distinctly auriculate, at least distal-most strongly reduced to ovate-triangular bracts with acute-acuminate apices, involucres without foliar bracts ..... **Grindelia inuloides**

1. Perennial, from a woody, fibrous-rooted corm; cauline leaves distinctly auriculate-clasping at base, distal not strongly reduced in size, similar in shape to those proximal, often continuing to immediately below involucres as foliar bracts ..... **Grindelia palmeri**

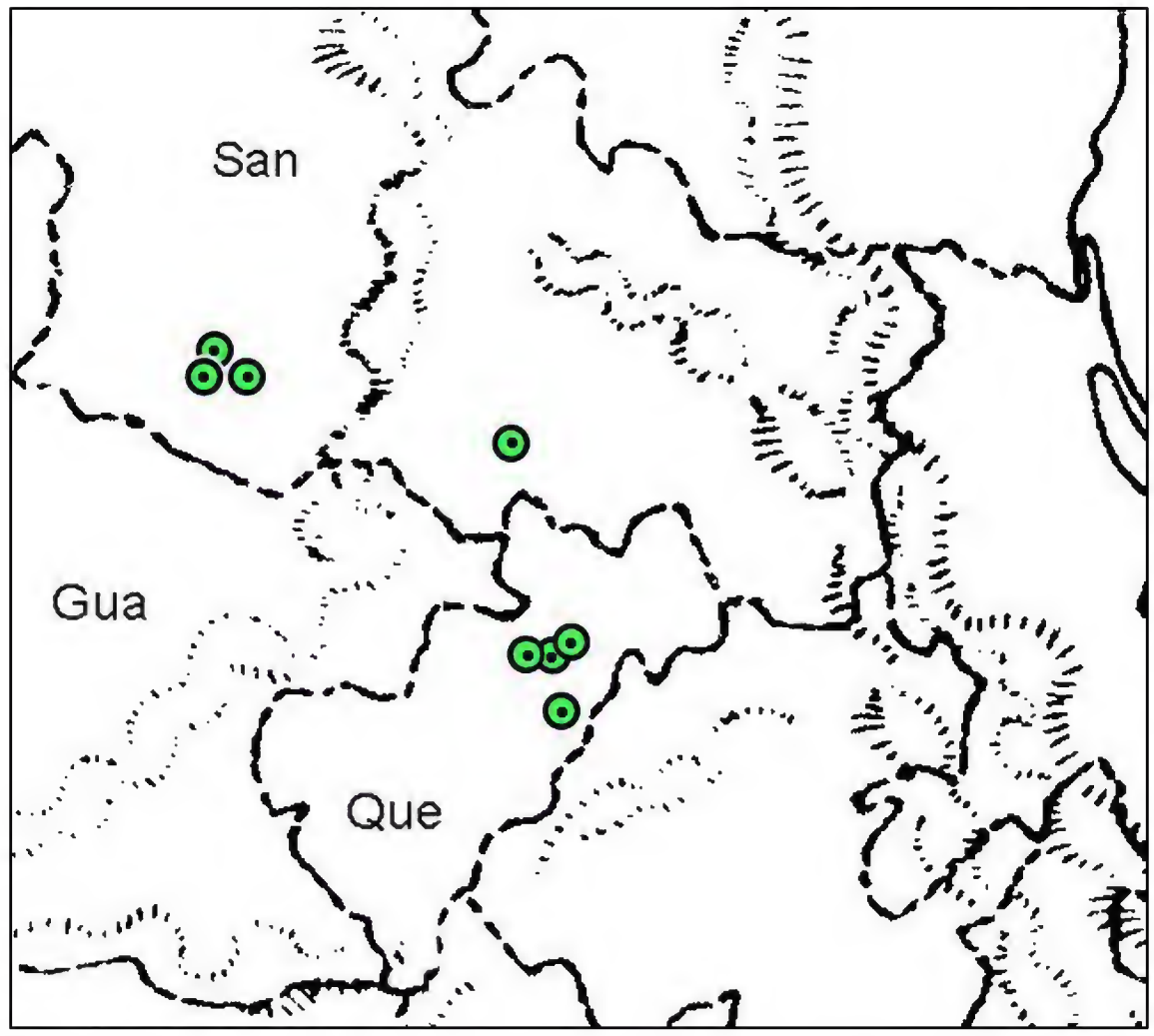

Figure 4. Distribution of *Grindelia palmeri*. Expected in the northeastern corner of Guanajuato.

2. GRINDELIA MACVAUGHII Nesom, Phytologia 68: 312. 1990. **TYPE**: **MEXICO**. **Jalisco**. [Mpio. Lagos de Moreno]: 15.9 km E of Agua El Obispo on Hwy 80, beside and in ditch on NW side of road, 1770 m, 29 Aug 1979, *M.E. Lane 2594* (holotype: TEX; isotypes: MEXU, TEX).

Perennial, from a woody taproot. **Stems** 30–90 cm tall, glabrous to sparsely pilose, eglandular. **Leaves** 1.5–4(–5.5) cm long, 4–15(–25) mm wide, oblong to oblong-lanceolate or ovate-lanceolate, base truncate, clasping but not decurrent, surfaces glabrous, not punctate or only weakly so, marginal teeth spinulose or sharp-pointed, eglandular. **Involucres** 12–20 mm wide; phyllaries strongly graduated in length, inner 7–9 mm long, white-indurate except at the tip, outer loose, erect to spreading or reflexing. **Achenes** usually prominently sculptured even at early maturity, with prominent transverse incisions and longitudinal furrows; pappus awns smooth.

Flowering Jul–Oct (–Nov). Oak, oak-pine, secondary vegetation, pastizal, grasslands, pastures, roadsides, ditches, clay or rocky soil, often wet or poorly drained; 1780–2500 m.

Additional collections examined. Aguascalientes. Mpio. Jesús María: El Rinconcito, 23 km W de Ags., orilla de camino, 2250 m, 12 Aug 1996, *Cerda L. 5649* (MEXU image). Mpio. San Jose de Gracia: La Congoja, orilla de camino, 2500 m, 17 Oct 1973, *Rzedowski & McVaugh 847* (MEXU-2 sheets images). **Jalisco**. [Mpio. Colotlan]: Near Colotlan, 29 Aug 1897, *Rose 3608* (MEXU). Mpio. Lagos de Moreno: Ca. 11 mi SE of Lagos de Moreno, near hwy to León, 1900 m, 7 Sep 1952, *McVaugh 12820* (F, SMU); 11 mi SE of Lagos de Moreno, 16 Aug 1957, *Waterfall 13869* (SMU). Mpio. Tepatitlán: 1 km adelante del Crucero a Arandas carr. Tepatitlán-Pegueros, pastizal secundario en suelos mal drenados cerca de la carretera, 1780 m, 28 Jul 1978, *Guzmán & Carvajal 953* (MEXU image). Mpio. Valle de Guadalupe: Campo Charro, carr. 80, entre Pegueros y Valle de Gpe., campo abierto, terreno semi-inundado, 1800 m, 19 Jul 1988, *Rodriguez C. et al. 1292* (MEXU image). **Michoacan**. Mpio. Churintzio: La Joya Sanguijuelas, 1880 m, 15 Aug 1986, *Labat 17210* (MEXU image). Mpio. Penjamillo: El Encinal, terreno plano, parcela de cultivo, 1950 m, 23 Aug 1990, *Pérez & García 1632* (MEXU image). Mpio. Tlazazalca: Presa La Yerbabuena, pastizal, terreno plano, orilla de la presa, 1950 m, 8 Aug 1990, *Pérez & García 1605* (MEXU image). **Zacatecas**. Mpio. Juchipila: Cerro de Piñones, rancho de Lorenzo Magallanes, bosque de coniferas, bosque mixto de encino-pino, zona agricola, 2064 m, 21 Nov 1997, *Balleza C. 7867* (MEXU image); W de Pueblo Viejo, Sierra de Morones, Cerro de Piñones, rancho de Lorenzo Magallanes, 1 km N de la casa del rancho, rumbo a la Loma

de Enmedio, veg. secundaria, 2003 m, 16 Oct 1998, *Balleza C. 9668* (MEXU image). Mpio. Téul de González Ortega: Km 193, carr. Zacatecas-Guadalajara, aprox. 2 km al S del Lacandón, bosque de *Quercus*, orilla de un arroyo, 1890 m, 1 Aug 1997, *Balleza C. 6377* (MEXU image). Mpio. Momax: Momax, 10 km N de Tlaltenango, suelo casi rojo y pedregosos, 1900 m, 16 Aug 1983, *Hernandez M. 9382* (MEXU image); 2 km N de Momax, 10 km adelante de Tlaltenango, orilla del río, pastizal en campo abierto, 1800 m, 14 Aug 1983, *Santana & Hernandez 1253* (MEXU image).

The protologue (Nesom 1990) of *Grindelia macvaughii* described the plants as annual, but additional collections show that they apparently are perennial or at least biennial. The species is more widely distributed than first assumed. *Grindelia macvaughi* and *G. inuloides* are similar in their non-punctate leaves, but the two are allopatric (Fig. 8) and can be separated on the basis of a set of morphological features.

1. Stems glabrous, eglandular; distal cauline leaves not strongly reduced, similar in shape to those proximal; leaf margins strongly scabrous, surfaces glabrous; achenes subquadrate, with prominent transverse incisions and broad, shallow, longitudinal furrows ..... **Grindelia macvaughii**

1. Stems sparsely villous or pilose, sometimes glandular; at least distal-most cauline leaves reduced to ovate-triangular bracts with acute-acuminate apices; leaf margins glabrate, surfaces minutely and sparsely appressed-puberulent; achenes slightly flattened to 3-angled, smooth or with distinct transverse incisions near the top ..... **Grindelia inuloides**

Grindelia macvaughii is similar to *G. palmeri* (see below) in its perennial duration and leaves with sharp-pointed, eglandular marginal teeth. They are allopatric (Figs. 4, 5) and separated morphologically as follows:

1. Perennial from a woody taproot; involucres without foliar bracts; leaves with punctate-glandular surfaces, glabrous, base truncate-clasping, not auriculate ..... **Grindelia macvaughii**

1. Perennial from a woody, fibrous-rooted corm; involucres usually with foliar bracts; leaves often with hirtellous and stipitate-glandular surfaces, base auriculate-clasping ..... **Grindelia palmeri**

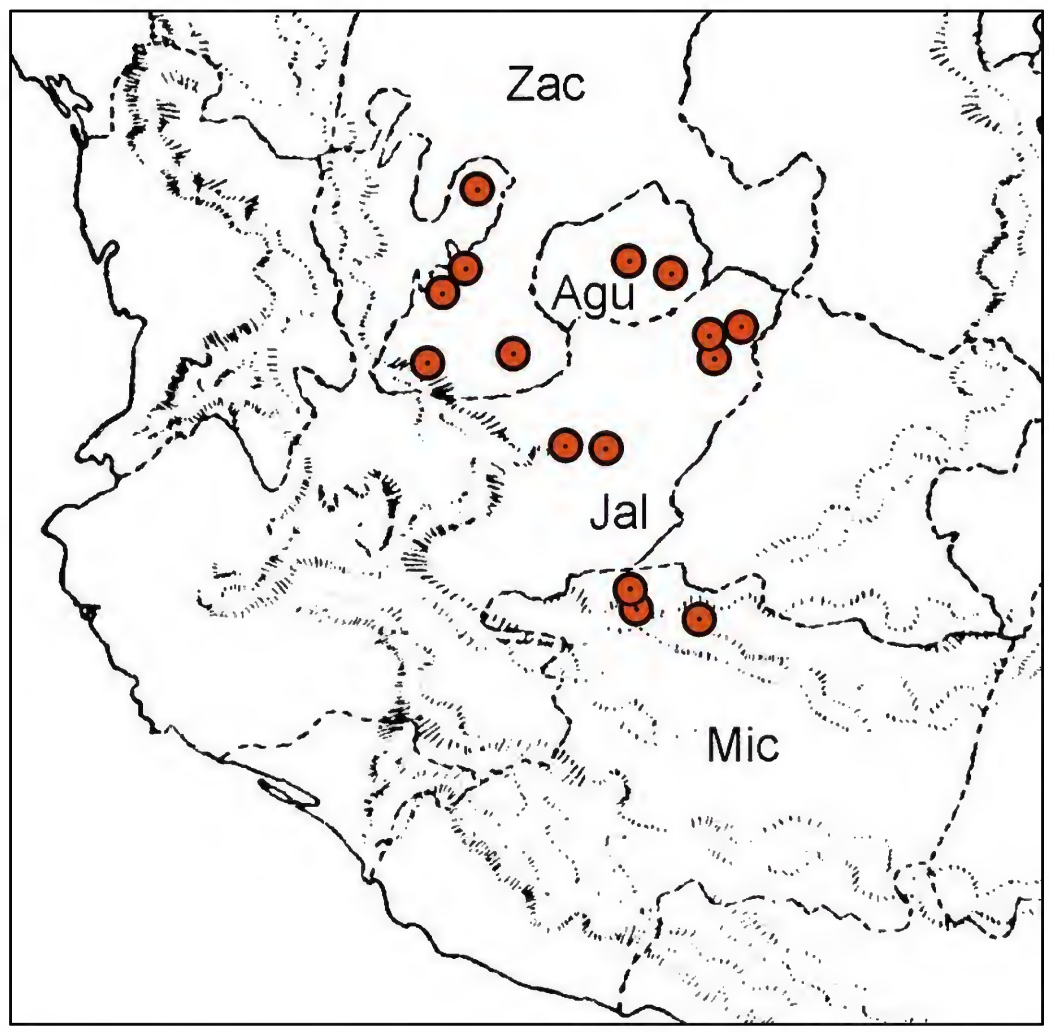

Figure 5. Distribution of *Grindelia macvaughii*. See allopatry of *G. macvaughii* and *G. inuloides* in Figure 6.

Figure 6. Representative morphology of *Grindelia macvaughii*. Top left: *Balleza C. 10344*, Zacatecas. Bottom left: *Rzedowski & McVaugh 847*, Aguascalientes. Right top and bottom: *Balleza C. 9668,* Zacatecas, a large-leaved form.

Figure 7. *Grindelia inuloides*, representative plant showing characteristic distal bracts. Hidalgo, *Pringle 6962* (MEXU, isotype of *Grindelia glandulosa* Greenman).

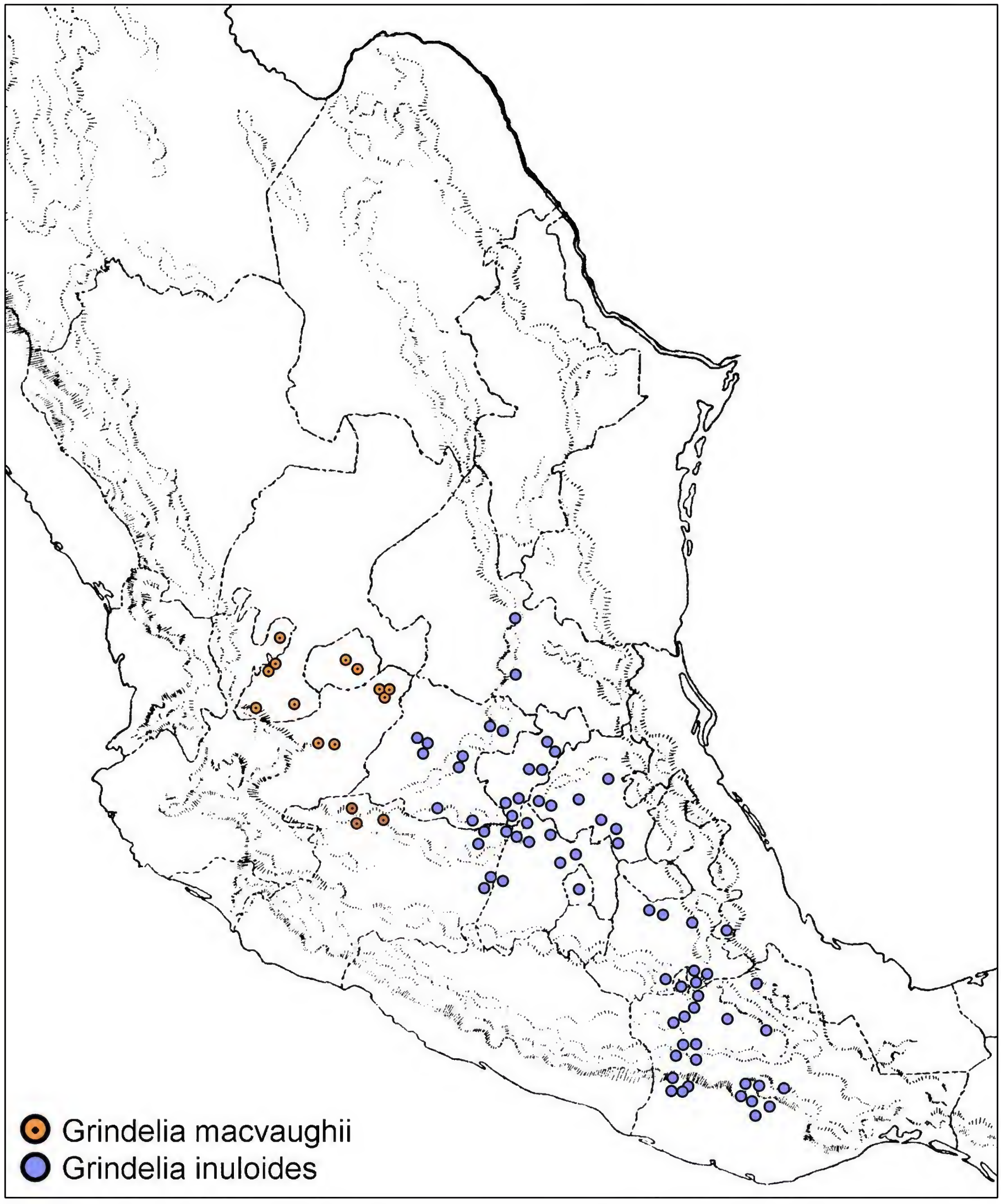

Figure 8. Distribution of *Grindelia inuloides* and *G. macvaughii*. Plants with stipitate-glandular leaves, distal stems, and phyllaries are scattered through the range of *G. inuloides* — the name *G. inuloides* var. *glandulosa*, which has been applied to these, is regarded here as a synonym of typical *G. inuloides*, the glandular plants as populational variants. Variants of *G. inuloides* in Oaxaca have been named as *G. inuloides* var. *hirtella* / *G. hirtella* — the taxonomy of the Oaxaca system, will be treated in a forthcoming study. Plants of Nuevo León and Coahuila identified as *G. inuloides* are not that species (Nesom in prep.).

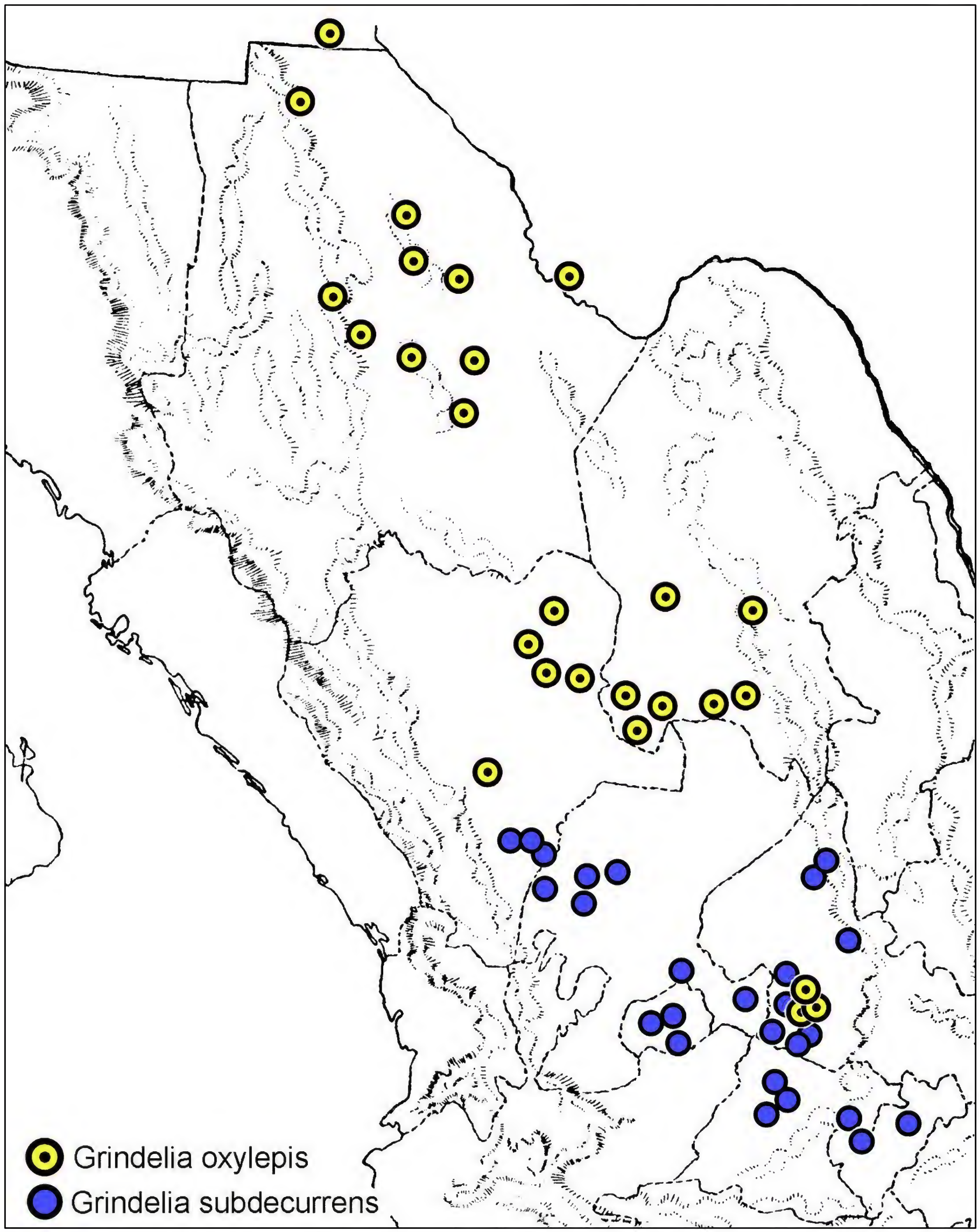

Figure 9. Distribution of *Grindelia subdecurrens* and *G. oxylepis*. Localities for *G. oxylepis* in Texas (Presidio Co.) and New Mexico (Dona Ana Co.) are from Nesom (1990) and Spellenberg (2014). See text for citations of collections from the vicinity of Cd. San Luis Potosí, where the perhaps are adventive.

3. GRINDELIA SUBDECURRENS DC., Prodr. 5: 315. 1836. **TYPE**: **MEXICO**. **Guanajuato**. [Mpio. Guanajuato]: Villalpando, 1829, *J. Mendez s.n.* (holotype: G-DC image!; isotype: GH!).

Perennial, taprooted. **Stems** mostly 0.3-1 m tall, usually with several ascending branches from the base, glabrous (sometimes hairy in Gua). **Leaves** oblong to oblong-lanceolate or ovate-triangular, cauline 10–22 mm long, (3–)5–12 mm wide, decreasing in size distally, base clasping, not decurrent or slightly so, surfaces prominently punctate, often resinous-sticky, glabrous except for scabrous margins, with blunt (rarely slightly sharpened), gland-tipped teeth. **Heads** solitary; phyllaries strongly graduated, apices punctate. **Achenes** monomorphic, slightly compressed or 3-angled, smooth until the last moments of ontogeny when prominent longitudinal furrows appear; pappus awns smooth edged. 2n=12.

Dur, Zac, Agu, San, Gua, Que; pastizal, matorral, grassy areas in open juniper woods, oak woods, roadsides, roadcuts, 1100–2620 m; (Jun–) Jul–Oct.

Leaves of *Grindelia subdecurrens* and *G. oxylepis* have punctate surfaces and margins with blunt, gland-tipped teeth — they can be separated by the following contrasts:

1. Annual, usually single-stemmed from the base, basal leaves deciduous by flowering; cauline leaves mostly 8–15 mm long, 3–5 mm wide, 2–2.5(–5) times longer than wide; achenes with deep transverse and longitudinal furrows (irregularly blocky) at early maturity (see Fig. 8) ..... **Grindelia oxylepis**

1. Perennials, usually several-stemmed from the base, basal leaves often persistent; cauline leaves mostly 10–22 mm long, 5–12 mm wide, 2.5–5 times longer than wide; achenes smooth at early maturity, developing longitudinal furrows at late maturity ..... **Grindelia subdecurrens**

The apparently disjunct occurrence of *Grindelia oxylepis* in San Luis Potosí (Fig. 9) is documented by the collections cited here. Mpio. Villa Hidalgo: Ca. 20 mi NW of SLP on Hwy 57 to Matehuala, 9.8 mi S of RR crossing at Ventura, *Nesom 6660* (TEX). [Mpio. San Luis Potosí]: Along Mex Hwy 57, 12.1 mi NNE of the Benito Juarez Monument in San Luis Potosí, scarce to common along roadside in disturbed loamy soil, 6 Aug 1983, *Freeman & Wetter 2072* (MEXU image); 8.7 mi N of San Luis Potosí, *Kral 27380* (MO); 8 km E de San Luis Potosí, terrenos inundables, 1850 m, 8 Jul 1959, *Rzedowski 11234* (MEXU image).

Figure 10. *Grindelia oxylepis*, Dona Ana Co., New Mexico. Pappus awns have been shed. From Spellenberg (2014), used by permission.

Figure 11. *Grindelia subdecurrens*, G DC holotype.

Figure 12. *Grindelia subdecurrens*, GH isotype. Leaves with punctate surfaces and blunt, gland-tipped marginal teeth.

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TAXONOMY OF *GRINDELIA LANCEOLATA* SENSU LATO (ASTERACEAE)

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ABSTRACT

The concept of *Grindelia lanceolata* Nutt. has sometimes included up to four varietal taxa — three of them are recognized here at specific rank and one is treated as a synonym of *G. decumbens*. **Grindelia lanceolata** sensu stricto occurs most abundantly in Missouri, Oklahoma, Arkansas, with numerous scattered outliers east of the Mississippi River and in southeast Texas. **Grindelia texana** Scheele occurs mostly on the Edwards Plateau of Texas and in northeastern Coahuila, Mexico. **Grindelia greenei** Steyerm. is a rare species endemic to the area of Monterrey, Mexico, and its immediate environs. *Grindelia subincisa* Greene is treated without formal taxonomic status within **G. decumbens** Greene of Colorado and New Mexico. The four taxa are mapped.

In taxonomic studies of *Grindelia* from Mexico and New Mexico, plants that have been identified as *G. lanceolata* Nutt. need review because of contrasting taxonomic treatments. The species has sometimes included up to four varietal taxa — three of them are recognized here at specific rank and one is treated as a synonym of *G. decumbens* Greene.

1. GRINDELIA LANCEOLATA Nutt., J. Acad. Nat. Sci. Philadelphia 7: 73. 1834. **LECTOTYPE** (Steyermark 1934, p. 515; not Bartoli & Tortosa 2012): [**Oklahoma**. Probably Muskogee or Wagoner Co., July-Aug 1819], *Z. Pitcher s.n.* (PH!; probable isolectotypes: BM image, NY image). See labels in Fig. 1. Protologue: "In Arkansas, T. Nuttall and Dr. Pitcher."

Steyermark cited the PH sheet as "type" in 1934 (ARKANSAS: "locality lacking, *Pitcher* [PA TYPE, NY]"), so the recent choice by Bartoli and Tortosa was superfluous.

Dr. Zina Pitcher was stationed as an army surgeon from November 1831 to July 1834 at Ft. Gibson, in what is now the northeast corner of Muskogee Co., Oklahoma (part of what was known as "Arkansas Territory" until 1836) and most of his collections probably were made in the vicinity of Ft. Gibson (McKelvey 1955). In 1833 he was part of a group building a portion of road from Fort Towson (in what is now Choctaw Co., Oklahoma) to Fort Smith, Arkansas (Fay 1975) and collected fossils of ammonites and oysters on the calcareous plains of the Kiamichi River (tributary of the Red River) in Choctaw County. He sent the fossils to the Academy of Natural Sciences of Philadelphia, where the ammonite was described in an 1834 publication — Pitcher also made collections of *Salvia* and *Corydalis* from "Red River, Arkansas" (see GH Herbarium 2019). He apparently sent his main set of vascular plant collections to PH, as they were significant in descriptions by Nuttall (1834) of new taxa.

Nuttall collected *Grindelia lanceolata* in eastern Oklahoma in 1819. In May and early June he was near the Red River in Choctaw County; from July into August he collected around Ft. Gibson, along the Verdigris River between Tulsa and Fort Gibson (in Muskogee, Wagoner, and Rogers counties), and up the Arkansas River to just west of Tulsa (Morrison 1926). His *G. lanceolata* collection almost certainly was made in the Ft. Gibson/Tulsa area, because the species flowers from late June through October. He later described (Nuttall 1834) a number of his own collections from eastern Oklahoma, citing his collections as types; he also based some of the new species on collections by Pitcher and some on collections by himself and later by Pitcher.

Grindelia lanceolata fma. *latifolia* Steyerm., Ann. Missouri Bot. Gard. 21: 516. 1934. **TYPE**: **USA**. **Missouri**. Stone Co.: Marble Cave, 11 Sep 1898, *W. Trelease s.n* (holotype: MO image).

Grindelia littoralis Steyerm., Ann. Missouri Bot. Gard. 21: 516. 1934. **TYPE**: **USA**. **Texas**. [Galveston Co.:] Evergreen [now known as Kemah], Galveston Bay, 20 Sep 1884, *J.F. Joor s.n.* (holotype: MO; isotypes: BRIT, ILL, MO).

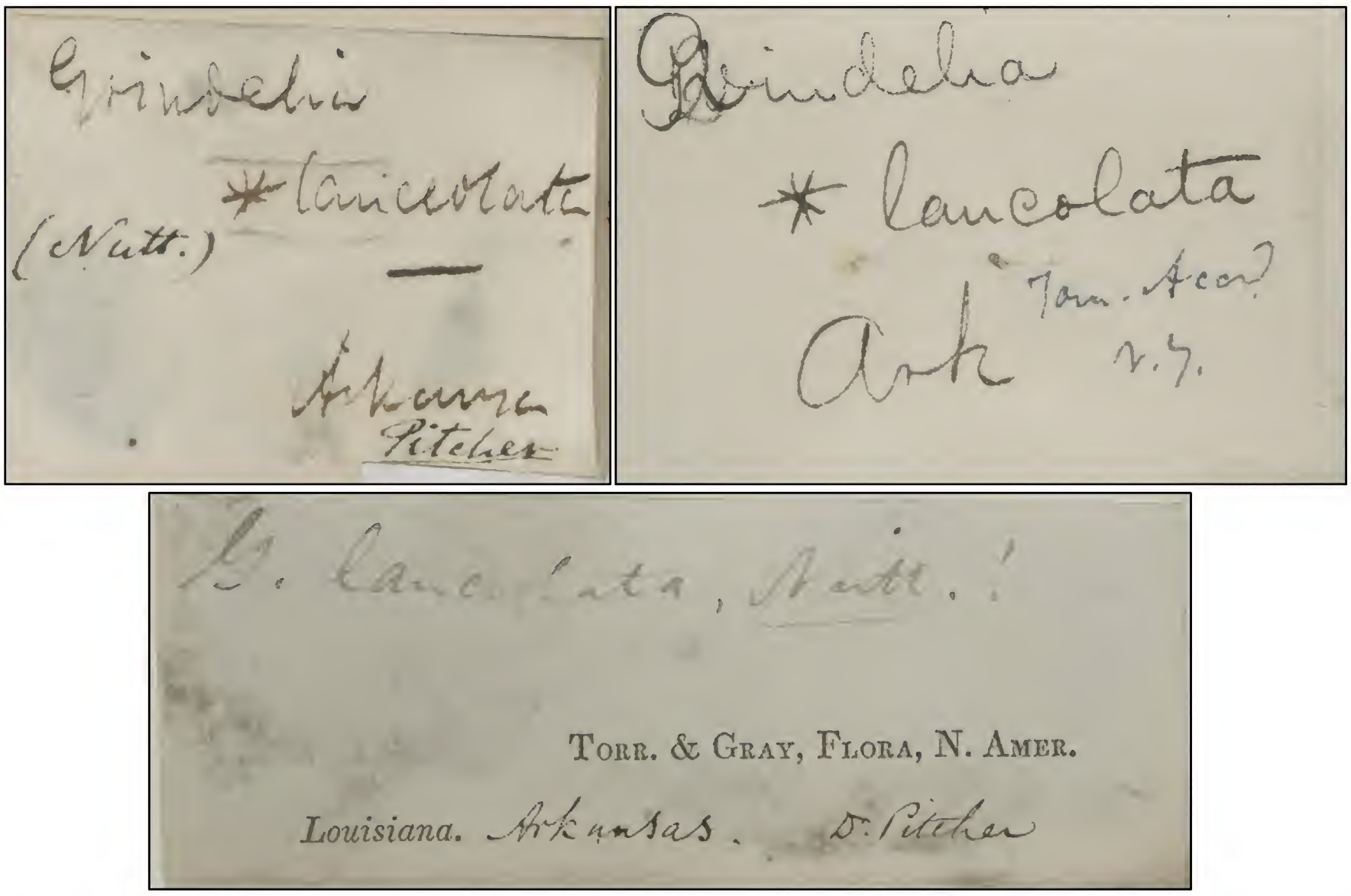

Figure 1. Labels for the type collection of *Grindelia lanceolata*. Top left: PH 00047860. Top right: BM 001050186 (perhaps not in Nuttall's hand?), mounted on same sheet as Drummond 137. Bottom: NY 00169613, mounted on same sheet as Drummond 137.

Steyermark (1934, p. 516) noted this for *Grindelia littoralis*: "This endemic of the Galveston Bay region is intermediate between *G. lanceolata* and *G. texana*. It possesses a larger amount of resin both on the leaves and involucre than either of the latter species; the leaf margins have teeth which are closely appressed and incurved, whereas in *G. texana* and *G. lanceolata* the teeth are directed outward and are more salient; the pappus awns in *G. littoralis* are mostly marked with several projections, whereas in the other two species they are entire or subentire." These features appear in various other localities and *G. littoralis* is interpreted.

The large leaves of *Grindelia lanceolata* fma. *latifolia* are distinctive but large-leaved variants appear sporadically elsewhere. Steyermark (1934, p. 516) noted that "This species is quite variable as to leaf shape, size, and margin, but the variations are not concomitant." Fma. *latifolia* also is regarded here as a populational variant.

Plants identified as *Grindelia lanceolata* from Chickasaw and Noxubee cos., Mississippi, and from Hale and Sumter cos., Alabama, are *Heterotheca camporum*. Collections identified as *G. lanceolata* from Potter Co., Texas, are *Rayjacksonia annua* (*Higgins 12507*, DES; *Higgins 11466*, UTC). Similarly, from Oklahoma, apparently the only collection from Harmon Co. is *Grindelia nuda* (IND, UTC); a collection from Canadian Co. is *Grindelia ciliata* (*Kiddie 63*, OCLA); a OKLA

collection from Woodward Co. proved to be a specimen of *Gaillardia*, mistakenly databased as *G. lanceolata*. A wool mill collection from South Carolina was from an introduced plant (Nesom 2004); disjunct occurrences in Virginia and North Carolina presumably are introduced (Weakley 2015). Plants from disjunct localities in Wisconsin (Dane Co., *Larsen s.n.*, WIS) and Ohio (Athens Co., *Porter & Wamsley 2116.1*, OS) were collected apparently in natural habitats and are considered here, tentatively, as native.

2. GRINDELIA TEXANA Scheele, Linnaea 21: 601. 1848. *Grindelia lanceolata* var. *texana* (Scheele) Shinners, Field & Lab. 19: 78. 1951. **LECTOTYPE** (designated here, superceding the choice by Bartoli & Tortosa 2012): **USA**. **Texas**. [Comal Co.:] New Braunfels, "sparsely on stony prairies, 2-4 ft high, only branching above," Aug 1846, *F. Lindheimer* Flora Texana exsiccata *418* (GH 283064 image; isolectotypes: G, GH-2 sheets, PH, US). Protologue: "Auf steiniger Prairie bei Neubraunfels: Lindheimer, August."

GH 283064 bears a handwritten label (by Lindheimer) identifying it as "Grindelia lanceolata var." and with collection data matching the protologue (Fig. 2): "Sparsely on stone prairies," "N Br" [New Braunfels], "Aug 46." The number "196," handwritten on the label, probably was Lindheimer's field number, different from his exsiccata numbering. The specimen also has an annotation by Asa Gray on one of his small "SYN. FL. N. AMER." labels as "forma spinulosa serrata," a phrase matching his description in Flora of North America (see next paragraph). The G, PH, and other two GH collections have only printed exsiccata labels, without Lindheimer's original notes that became part of the protologue. Bartoli and Tortosa chose the US collection as lectotype.

Torrey and Gray (1841, p. 248) recognized what would later be named as *Grindelia texana* as variety "γ.?" within *G. lanceolata* — contrasted to typical form by 'leaves short, oblong-lanceolate, partly clasping, spinulose-serrulate; scales of the involucre with shorter appendages, more unequal and appressed, … lower leaves incisely **spinulose-serrate**, or sometimes almost pinnatifid" and typified by "Texas, Drummond!" The Drummond collection almost certainly are the plants mounted with the BM and NY isolectotypes of *G. lanceolata*, as noted above.

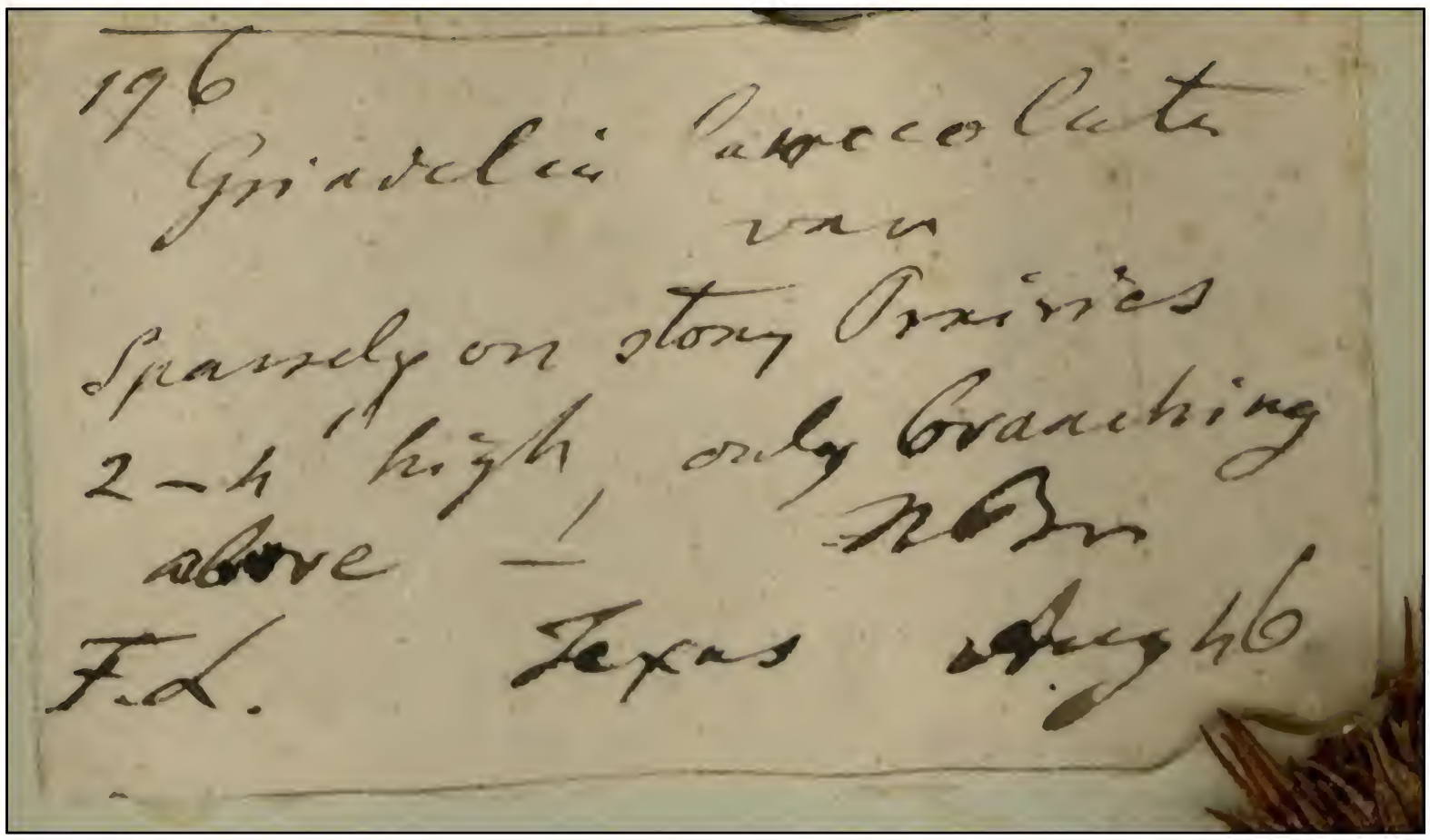

Figure 2. Handwritten label on the GH 283064 lectotype collection of *Grindelia texana*. This is the only one of the sheets of Lindheimer's collection with label data matching the protologue.

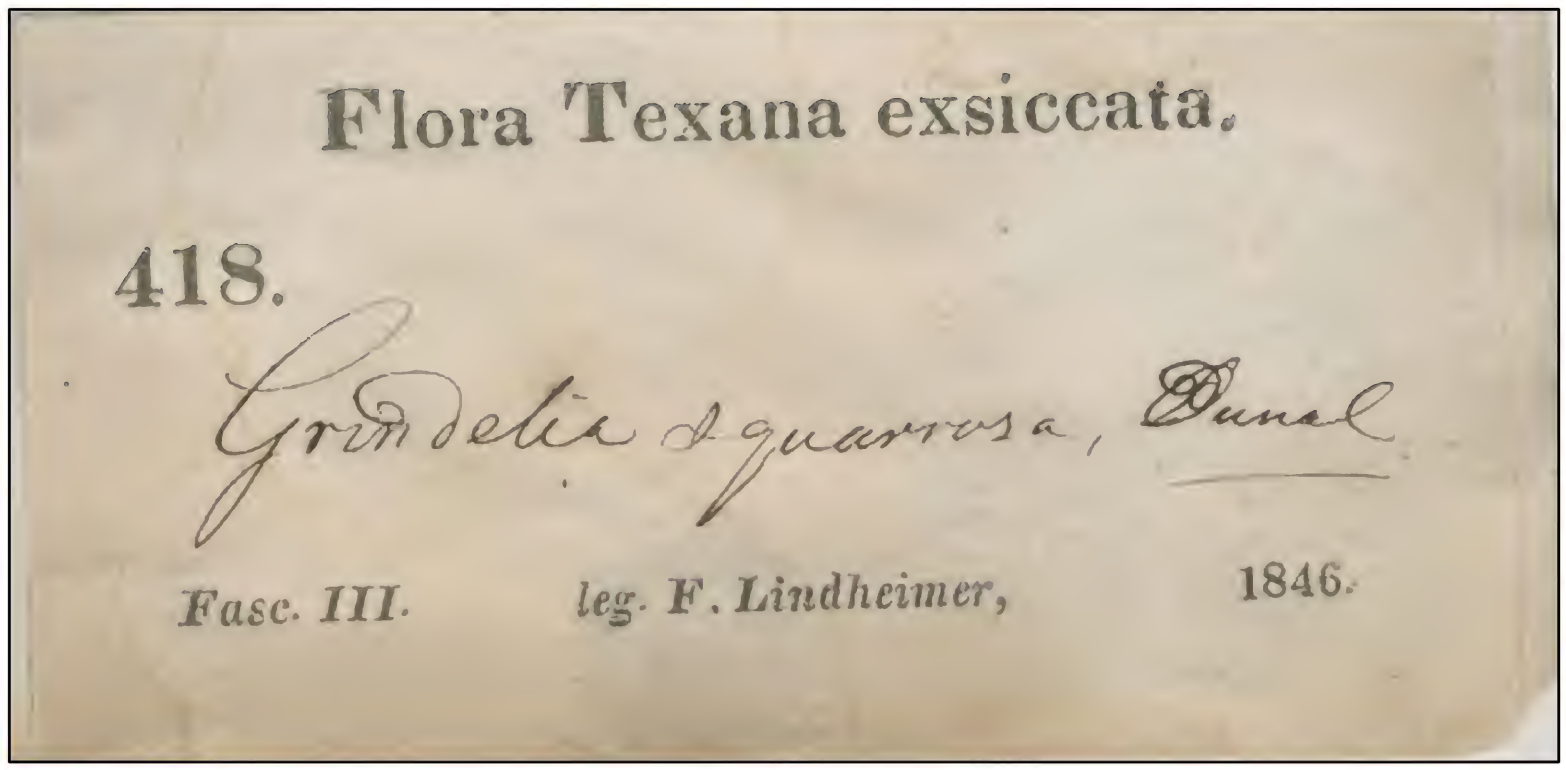

Figure 3. Label on the US type collection of *Grindelia texana*, selected by Bartoli and Tortosa as lectotype. The printed exsiccata label is the same as on the duplicates from G, GH, and PH.

Correll and Johnston (1970) included *Grindelia texana* as a synonym of *G. lanceolata*, but they noted that two morphological types exist in Texas (the *G. texana* type and "true *G. lanceolata*"; see comments below). Taylor and Taylor (1994) treated *G. texana* as a variety of *G. lanceolata*. Diggs et al. (1999) and Tyrl et al. (2009) included *G. lanceolata* but not *G. texana*, not even mentioning the latter as a synonym.

Shinners's reduction of *Grindelia texana* to varietal rank (1951) was accompanied by this comment: "Species and variety have the same habitat preferences and very small morphological differences (looking more distinct in print than in nature)." But while the differences may seem relatively small, they are consistent and mark distinct geographical entities. The sharply bounded eastern edge of the *G. texana* range coincides with the eastern boundary of the Edwards Plateau, and habitats are correspondingly distinct: rocky hills, bluffs, and ridges, limestone outcrops, prairies, and roadsides, upland clay and caliche — all characterized by a limestone substrate. Habitats of *G. lanceolata* also tend to be over calcareous substrate but are more diverse: limestone outcrops and glades, shell mounds, marsh, river, and stream banks, blackland, clay, and sandy prairies, forest openings, and rocky and gravelly roadbanks. Both taxa have chromosome counts of $2n = 12$.

Steyermark noted (1934, p. 516) that "In the vicinity of Dallas, Texas, a region of range overlap of *Grindelia texana* and *G. lanceolata* … collections have been taken which are intermediate between, and may be hybrids of *G. texana* and *G. lanceolata*." Correll and Johnston (1970, p. 1572) made a similar observation, noting that "The plants from most of Texas have rather large achenes and mostly deltoid leaves (*G. texana*), but in north-central Texas this type grades northward into a type (true *G. lanceolata*) with shorter achenes, shorter duration (biennial?) and more elongate leaves." Strother and Wetter (2006) also treated *G. texana* as a synonym but recognized the occurrence of the morphogeographic variant. The present study confirms apparent gene flow in the area of sympatry of *G. lanceolata* and *G. texana* around Dallas (Fig. 4) — Figure 8 show a collection where both species apparently were present, Figure 9 where plants apparently were intermediate.

Gene flow apparently occurs between *Grindelia lanceolata* and *G. texana* in their small area of sympatry, and some disjunct prairie plants of southeastern Texas seem to show 'texana' features (see Fig. 7) and a collection of typical *G. texana* was made in Hopkins Co., Texas (Fig. 15), about 80 miles east of the closest populations in the main range. The decision here to recognize *G. texana* at specific rank emphasizes its essential fidelity to the Edwards Plateau region and its consistent morphological difference from *G. lanceolata*.

The couplet below essentially follows Steyermark's concepts:

a. Annual or short-lived perennial; phyllaries subequal in length, outer about equalling the height of the disk; leaves mostly oblong to lanceolate-oblong or lanceolate, margins shallowly serrulate to serrate or crenulate, with (6–)10–20 pairs of teeth, distal narrowly lanceolate to lanceolate-linear; inner achene faces smooth or weakly longitudinally nerved ..... **Grindelia lanceolata**

a. Perennial; phyllaries graduated in length, outer less than 1/2 the height of the disk; leaves oblong or nearly elliptic to oblong-lanceolate, ovate-triangular or triangular, margins coarsely serrate with 3–8 pairs of aristate-spinulose teeth, distal usually ovate-triangular to ovate; inner achene faces with numerous, longitudinal, thin and superficial nerves ..... **Grindelia texana**

Collections of plants disjunct in northern Mexico are these. **Coahuila**. 21 km S by winding road from Rancho Chupadero del Caballo toward Las Norias, 12 Sep 1972, *Chiang, Wendt, & Johnston 9170* (NY); W slopes of Sierra del Carmen, 8 km E of Hacienda Encantada, 15 Sep 1941, *Stewart 1702* (GH).

3. GRINDELIA GREENEI Steyerm., Ann. Missouri Bot. Gard. 21: 517. 1934. *Grindelia lanceolata* var. *greenei* (Steyerm.) Nesom, Phytologia 68: 324. 1990. **TYPE**: **MEXICO**. **Nuevo León**. "Vicinity of Monterrey," 1924, *C.R. Orcutt 1204* (holotype: US image). Figure 16.

Additional collections examined. **MEXICO**. **Nuevo León**. Monterrey, "foot Chipinque," 9 Oct 1937, *Kenoyer 300* (F, MO); Monterrey, 1924, *Orcutt 1249* (US).

Grindelia greenei has been known by only three collections, as cited above, from Monterrey and close-by localities, but its continued existence is recently confirmed. Recent photos posted on Naturalista (2019) show it from two other sites, both also very near Monterrey (just west of García, southwest of Picachos el Fraile — photos by Carlos Velazco, see Fig. 17; Santa Catarina — photos by Tadeo Hernández). Nesom (1990) treated *G. greenei* at varietal rank within *G. lanceolata*, but the collections and photos show that its morphology is constant and distinct from *G. lanceolata*, and the disjunction of about 250 miles (Fig. 4) from both *G. lanceolata* and *G. texana* supports its recognition at specific rank.

Characteristic features: glabrous vestiture, leaves prominently punctate on both surfaces; leaves broadly oblong to broadly ovate-elliptic or lanceolate-oblong, 15–25 mm long, nearly even-sized up to the heads or slightly reduced, base truncate, apex rounded to rounded-obtuse, margins with 10–15 pairs of sharp-pointed but not spinulose teeth; involucres 10–12 mm wide; phyllaries distinctly graduate in length.

4. GRINDELIA DECUMBENS Greene, Pittonia 3: 102. 1896. *Grindelia hirsutula* var. *decumbens* (Greene) Ackerf., Fl. Colorado, ix. 2015. **TYPE**: **USA**. **Colorado**. [Montrose Co.]: Cimarron, 30 Aug 1896, *E.L. Greene s.n.* (holotype: NDG-53581; isotype: NDG-53582).

Grindelia subincisa Greene, Pittonia 4: 154. 1900. *Grindelia decumbens* var. *subincisa* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 503. 1934. *Grindelia lanceolata* var. *subincisa* (Greene) Bartoli & Tortosa, Ann. Missouri Bot. Gard. 98: 480. 2011 [2012]. **LECTOTYPE** (Bartoli & Tortosa 2012): **USA**. **New Mexico**. [Rio Arriba Co.]: Chama, 5 Sep 1899, *C.F. Baker 683* (NDG-47371; isolectotypes: F, GH, NDG, NY, RM, RSA, US-2 sheets).

Bartoli and Tortosa (2012) transferred the mainly Colorado taxon *Grindelia subincisa* to *G. lanceolata* at varietal rank. Steyermark (1934), followed by Harrington (1954) and Martin and Hutchins (1980) placed *G. subincisa* as a variety within *G. decumbens*, while Allred and Ivey (2012) treated *G. subincisa* simply as a synonym within *G. decumbens*. Ackerfield (2015) treated *G. decumbens*, presumably including var. *subincisa*, at varietal rank within *G. hirsutula* Hook. & Arn., in its strict sense an endemic of California coastal ranges. Strother and Wetter (2006), however, enlarged

the concept of *G. hirsutula* by including within it about 30 taxa regarded as distinct by most other botanists. Strother and Wetter maintained *G. decumbens* as distinct; Ackerfield's taxonomic combination followed suit in *G. hirsutula* and further broadened its concept.

In allying *Grindelia subincisa* with *G. lanceolata*, Bartoli and Tortosa (2012) pointed out differences between *G. decumbens* and *G. lanceolata* (phyllary shape and degree of graduation and leaf tooth apex) but did not say on what basis they saw an intimate connection between *G. subincisa* and *G. lanceolata*. Within the larger population system of *G. decumbens*, even within single populations, morphology of leaf teeth and involucres varies and there appears to be no unarbitrary geographic or morphological way to recognize infraspecific entities (i.e., "subincisa") within what is identified here as *G. decumbens*. In addition to the wide geographic hiatus beween *G. decumbens* and *G. lanceolata* (Fig. 4), diagnostic morphological differences are apparent — *G. decumbens* is shorter in stature, has smaller, hemispheric-campanulate involucres, and has graduated phyllaries with an abruptly narrowed-acuminate and reflexed apical region (Figs. 18, 19).

Plants IDed on SEINET and in databases as *Grindelia decumbens* from Fremont and Mesa counties, Colorado, and from Grant and Hidalgo counties, New Mexico, are not *G. decumbens*.

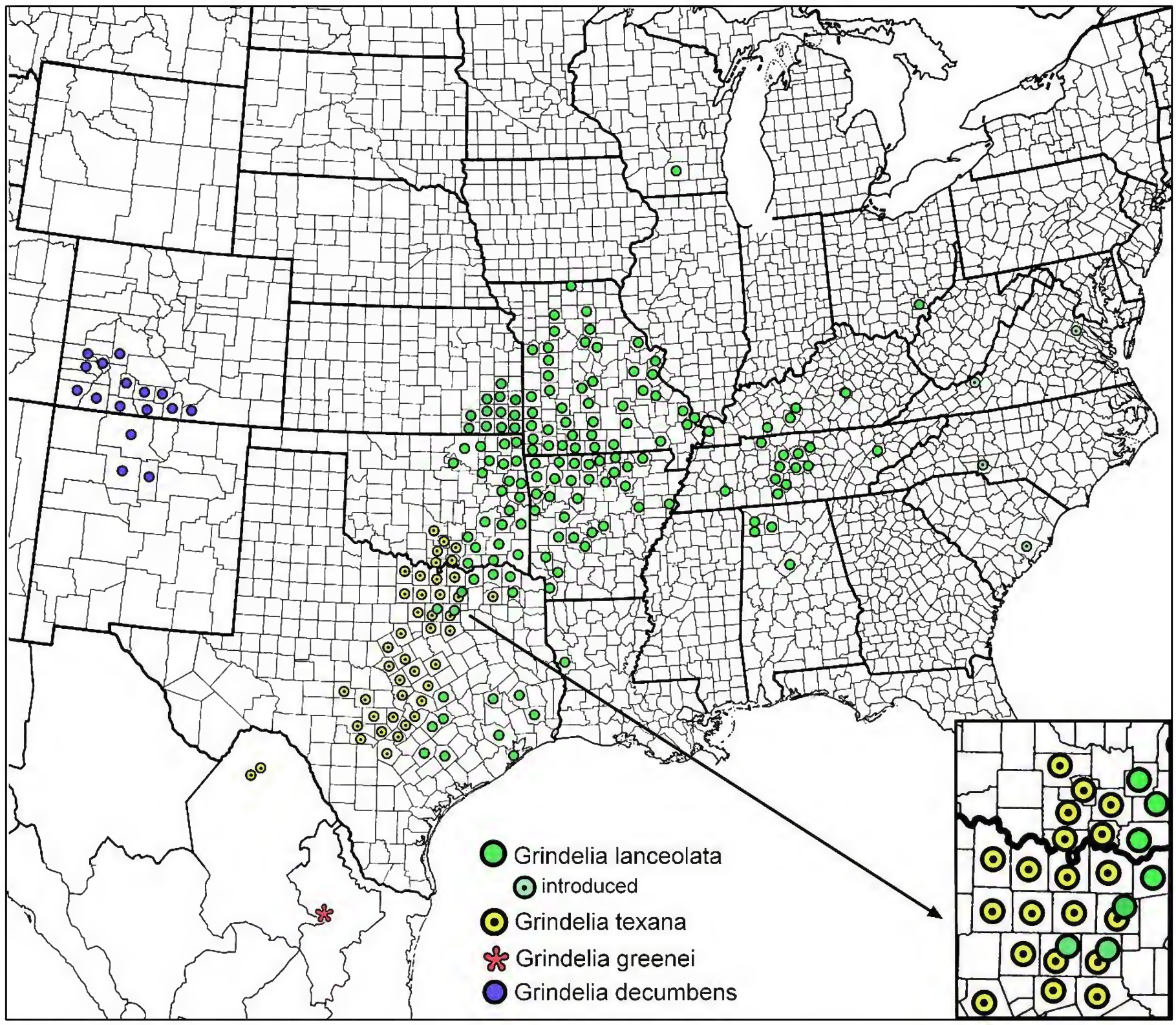

Figure 4. Distribution of *Grindelia lanceolata*, *G. texana*, *G. greenei*, and *G. decumbens*. Inset shows enlarged area of sympatry between *G. lanceolata* and *G. texana* — Collin, Dallas, and Tarrant counties. The eastward-disjunct collection of *G. texana* from Hopkins Co., Texas, is shown in Figure 15.

Figure 5. *Grindelia lanceolata*, representative morphology. Bastrop Co., Texas, *Neff 02061103* (TEX).

Figure 6. *Grindelia lanceolata*, representative morphology. Polk Co., Texas, *Hillhouse s.n.* (TEX).

Figure 7. *Grindelia lanceolata*, representative morphology. Edmonson Co., Kentucky, *Medley & Cassel 14450-86* (ASPC).

Figure 8. *Grindelia lanceolata* (left) and *Grindelia texana* (right), apparently a mixed population. Dallas Co., Texas, *Biltmore 14926* (IND).

Figure 9. *Grindelia lanceolata* x? *G. texana*, both stems perhaps intermediate, or closest to *G. texana* (compare *G. texana* in Fig. 14 from Wise Co.). Dallas Co., Texas, *Lundell 11556* (LL).

Figure 10. *Grindelia lanceolata* with incised-spinulose leaf margins and graduated phyllaries more characteristic of *G. texana*, from a disjunct prairie habitat. Hardin Co., Texas, *Lundell 11556* (LL).

Figure 11. *Grindelia texana*, representative morphology. Tarrant Co., Texas, *Byerly 524* (BRIT).

Figure 12. *Grindelia texana*, representative morphology. Hamilton Co., Texas, *Massey 341* (LL).

Figure 13. *Grindelia texana*, representative morphology. Brown Co., Texas, *Hansen 7402* (TEX).

Figure 14. *Grindelia texana*, variability of leaf margin within a population. Wise Co., Texas, *Orzell & Bridges 11285* (TEX).

Figure 15. *Grindelia texana*, typical morphology, eastward disjunct from the main range of the species (see Fig. 4). Texas, Hopkins Co.: 1 mi E of Mount Vernon, open roadside, 25 Jun 1949, *Stitelor s.n.* (PH).

Figure 16. *Grindelia greenei*, holotype.

Figure 17. *Grindelia greenei* from west of García, Nuevo León, just north of Monterrey. Photo by Carlos Velazco, 11 July 2007. From Naturalista 2019, used by permission.

Figure 18. *Grindelia decumbens*, representative morphology. Mesa Co., Colorado, *Trappett 86-52* (MESA).

Figure 19. *Grindelia decumbens*, representative morphology. Mineral Co., Colorado, *Regensberg 1943* (DBG-KHD).

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I'm grateful to Mark Fishbein for checking the identity of the Woodward Co., Okla., plant identified as *Grindelia lanceolata* and Rachel Jones for sending photos of the Canadian Co. collection, Carlos Velazco for permission to use the *in situ* photo of *G. greenei*, Ken Heil for help with literature, PH staff for their hospitality, and Art Gibson for detailed descriptions of achenes of *G. texana* and *G. lanceolata* from Williamson Co., Texas, as well as for the record of *G. lanceolata* from Milam Co.

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SENECIO FREMONTII SENSU LATO (ASTERACEAE) INCLUDES THREE SPECIES

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ABSTRACT

Senecio fremontii has usually been regarded as comprising four varieties, but here it is treated as three distinct species: *S. fremontii* Torr. & Gray, *S. blitoides* Greene, and **Senecio inexpectatus** (Cronq.) Al Schneid., **comb. et stat. nov.** *Senecio fremontii* var. *occidentalis* is treated as a synonym of typical *S. fremontii*. Each of the three species has a consistent morphology and geography — a county level map shows their distribution, and representative plants for each are illustrated by herbarium sheets. A taxonomic summary and key to the taxa are provided. A lectotype is designated for *Senecio occidentalis* var. *rotundatus* Rydb.

Senecio fremontii has been divided taxonomically into four varieties (e.g., Cronquist 1994, Barkley 2006): var. *fremontii* (northern Rocky Mountains and interior ranges), var. *blitoides* (Colorado, New Mexico, Wyoming), var. *occidentalis* (California and Nevada), and var. *inexpectatus* (east-central Utah). The habitat of each of these taxa is at high elevations, typically in alpine and subalpine sites sometimes down to high coniferous associations. It seems at least a reasonable assumption that they share an immediate common ancestor — all are glabrous, non-viscid perennial herbs with lax, relatively short stems, relatively small, thick to subsucculent, mostly cauline leaves (basal usually not persistent) with toothed margins. Cronquist (1994) characterized the Intermountain West plants as "eventually taprooted, although the branches of the caudex may become slender and rhizome-like." Barkley's corresponding key character (2006) was phrased as "taprooted with subrhizomatous caudices." The species note for var. *fremontii* by Welsh et al. (2015) says this: "Subterranean caudex and commonly naked soboliferous branches, that evidently finally root and become rhizomes are common features [of var. *fremontii*], but plants with caudex superficial or nearly so are present as well."

Cronquist and Barkley apparently have provided the only treatments of *Senecio fremontii* that include all four varieties — neither botanist, however, provided an explicit rationale for the taxonomic ranks. Cronquist (p. 172) noted only that the species "consists of four geographic varieties" — in his description of var. *inexpectatus* (p. 172), he made not a single comment except in the context of the key to varieties. Barkley (p. 564) noted that "The varieties are distinguished by morphologic tendencies plus their geographic ranges" — he observed that var. *fremontii* intergrades locally with *Senecio spartioides* in the mountains of the Great Basin" but did not mention intergradation among the *S. fremontii* varieties.

The current study was undertaken as a result of the discovery of *Senecio fremontii* var. *inexpectatus* Cronq. in Dolores Co., Colorado, disjunct about 80 miles southeast from the main Utah population system (Figs. 1, 2, 3). The type of var. *inexpectatus* is from the La Sal Mountains, where the taxon occurs abundantly and where it had been thought to be endemic. In an attempt to understand the evolutionary position of var. *inexpectatus*, a study of variation over *S. fremontii* (sensu lato) has led to the conclusion that three of the four named varieties are justifiably treated at specific rank: *S. fremontii*, *S. blitoides*, and *S. inexpectatus*. *Senecio fremontii* var. *occidentalis* is treated as a synonym of typical *S. fremontii*.

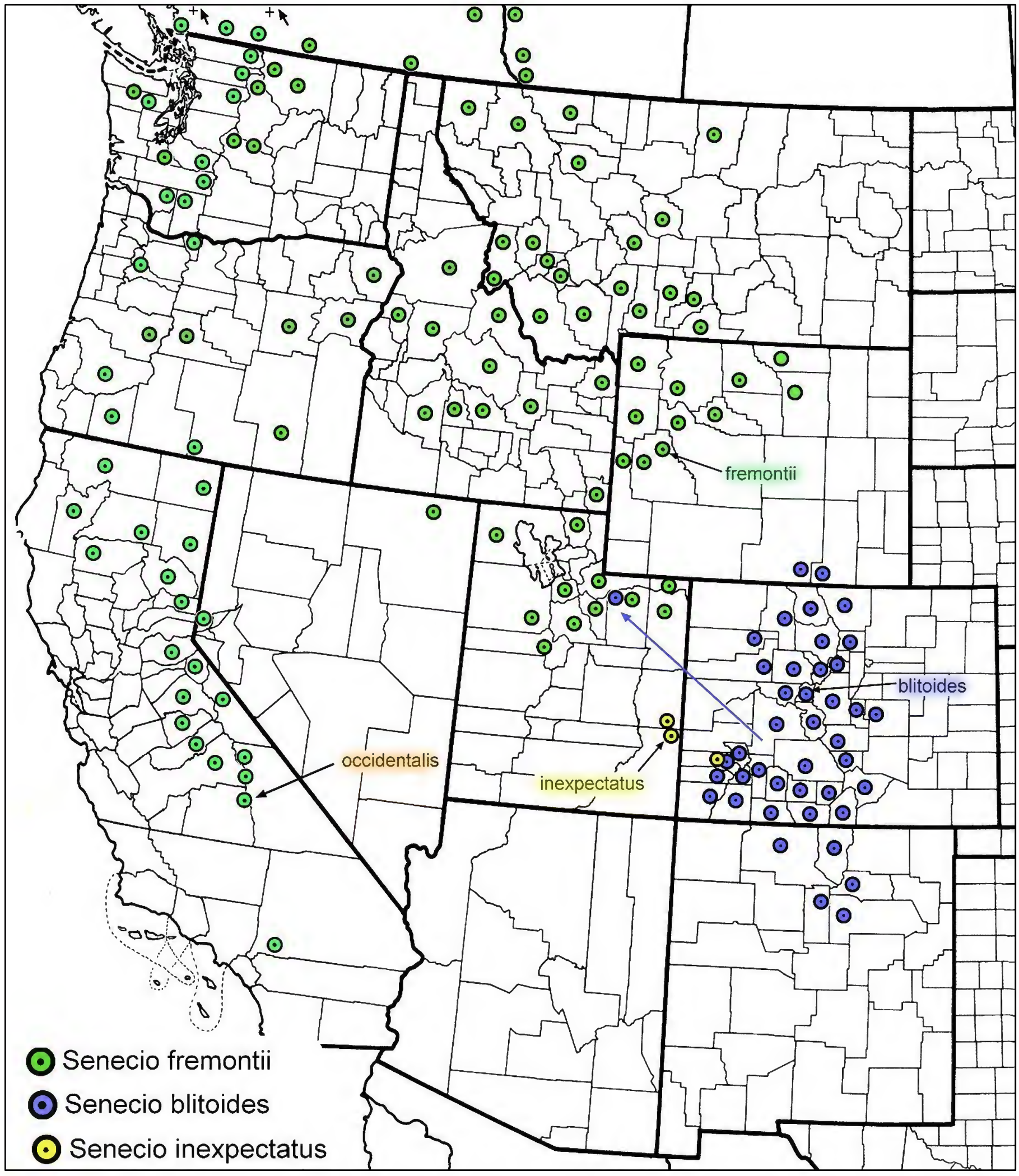

Figure 1. Distributions of *Senecio fremontii* (including *S. occidentalis*), *S. blitoides*, and *S. inexpectatus*. Records are mostly from databases (via SEINet and Consortium of PNW Herbaria); in most cases, identities have been verified through a voucher or an image. Black arrows indicate type localities. The blue arrow points to a disjunct locality in Utah for *S. blitoides*.

Morphological distinctions reported between var. *occidentalis* and var. *fremontii* (involucre size, cauline leaf distribution) are not consistent. The smallest involucres appear in California, but the whole range of size variation noted in the key below also occurs there. A similar range of variability in peduncle length occurs over the whole range of *S. fremontii*.

Compared to *Senecio fremontii*, *S. blitoides* and *S. inexpectatus* as a pair are consistent between themselves in easily observed traits: plant habit, leaf morphology and cauline distribution, features of marginal teeth, involucre size, and number of ray flowers. They probably are evolutionarily sister taxa.

The key below documents morphological contrasts among the three species identified in the current study.

1. Stems usually decumbent-ascending from the base, often rhizomatous proximally; cauline leaves ending distally well below heads, heads on distinct, bracteate or ebracteate peduncles; leaf usually petiolate to subpetiolate, sometimes epetiolate, base never subclasping; leaf margins sparsely serrulate to coarsely serrate, dentate-serrate, or shallowly lobed, teeth acute, not sharp-pointed and spinulose, often indurate; involucres 7–10 mm high, 7–10(–11) mm wide; ray flowers (7–)8(–9) ..... **Senecio fremontii**

1. Stems usually erect to ascending-erect from the base, sometimes proximally subrhizomatous; cauline leaves continuing distally to immediately below heads; leaf sessile, base usually truncate to rounded or acute to acuminate, epetiolate, sometimes subclasping; leaf margins dentate to dentate-serrate or laciniate or laciniate-dentate, teeth sharp-pointed and spinulose or subspinulose; involucres 8–12 mm high, 9–13 mm wide; ray flowers 8–11 or (12–)13(–14).

   2. Leaf margins laciniate to laciniate-dentate; involucres 8–10(–12) mm high, 9–12 mm wide; ray flowers 8–11 ..... **Senecio inexpectatus**

   2. Leaf margins mostly dentate to dentate-serrate; involucres 9–11 mm high, 9–13 mm wide; ray flowers (12–)13(–14) ..... **Senecio blitoides**

1. **SENECIO INEXPECTATUS** (Cronq.) Al Schneid., **comb. et stat. nov.** *Senecio fremontii* var. *inexpectatus* Cronq., Intermount. Fl. 5: 172, pl. s.n. [p. 173, upper left]. 1994. **TYPE**: **Utah**. San Juan Co.: La Sal Mts., along the rocky, granitic crest of the ridge leading from Mt. Peale toward Mt. Mellenthin and Mt. Tukuhnikivatz, SE of Moab, 12,200 ft, 9 Jul 1961, *A. Cronquist & N. Holmgren 9464* (holotype: NY image).

The nomenclatural combination is made here (in Nesom) by Al Schneider, who discovered the Colorado population of these plants, identified them correctly, and recognized that they probably deserved to be recognized at specific rank. Al is the author, editor, and publisher of the Southwest Colorado Wildflowers website (Schneider 2019).

The morpho-geographic distinction of *Senecio inexpectatus* from *S. blitoides* and especially from *S. fremontii* sensu stricto is unambiguous (Figs. 1–9). Occurrence of *S. inexpectatus* in sympatry with *S. blitoides* in Dolores Co., Colorado, supports its recognition at specific rank. Plants of *S. blitoides* occasionally produce leaves with deeply toothed margins (e.g., Figs. 11, 12, 13, 19); none are consistently laciniate as in *S. inexpectatus* and the difference in ray number is consistent.

Additional collections. **Colorado**. Dolores Co.: Cross Mountain Trail, 1/4 mi S of jct with Lizard Head Trail, on gray shale, with *Penstemon harbourii*, *Smelowskia calycina*, *Mertensia lanceolata*, *Trifolium attenuatum*, *Aquilegia coerulea*, *Erysimum capitatum*, 7 Jul 2008 (vegetative), *Schneider s.n.* (COLO); Cross Mountain Trail, on Mancos Shale, 11,700 ft, 19 Aug 2008, *Schneider s.n.* (COLO). **Utah**. Grand Co.: LaSal Mts.: NW corner of Beaver Basin above mine tunnels, subalpine meadows, ca. 11,000 ft, 22 Aug 1985, *Franklin 2282* (BRY); mid-slope up W side of Prospect Peak, 38° 31° 32° N, 109° 14° W, alpine cushion plant community, gravels, 11,640 ft, 28 Aug, 2013, *Huber 5352* (BRY, UTC); Horse Gulch and vicinity, 3000-3200 m, 15 Jul 1911, *Rydberg & Garrett 8961* (NY). San Juan Co.: La Sal Mts.: Forest Rd 241, Gold Basin, high mountain meadow, base of diorite scree slope amid large boulders, 10,044 ft, 2 Aug 2005, *Barnes 4706* (UVSC); E flank of Mt. Mellenthin, W side of road, mixed coniferous forest, semi-barren steep open slope, rocky, E aspect, 3400 m, 4 Sep 1999, *Delmatier 8128* (BRY); Dark Canyon, S-facing talus-gravel slope, 11,000 ft, 18 Jul 1984, *Franklin 910* (BRY); ridge between Mt. Mellenthin and Mt. Peale, on bedrock, 26 Jul 1985, *Franklin 2039* (BRY); along ridge ca. 1.1 mi N of Mt. Peale, fine gravel slope into Gold Basin, 11,920 ft, 24 Jul 1986, *Franklin 3946* (BRY); 1.1 mi NNW of Mt. Peale, along ridge above

Dark Canyon, rocky, talus slope, 12,000 ft, 15 Sep 1986, *Franklin 4288* (BRY); Dark Canyon Road (FS Road 126), 3.5 mi S of Geyser Pass, spruce-fir forest, road cut on N-facing slope with damp soil, 10,470 ft, 18 Jul 2012, *Goodwin 3508* (ASC); Dark Canyon, 0.5 mi NW of Mt. Peale, alpine plant community, on sloughing, rocky slope near a stream, 11,405 ft, 27 Aug 2013, *Huber 5327* (BRY, MO, NY, UT, UTC); ridge between Mt. Tukuhnikivatz and Mt. Peale, S slope of ridge, patches of alpine meadow among talus, 11,201 ft, 27 Jul 1982, *Siplivinsky 4347* (CM, COLO, UCR); ca. 19 mi SE of Moab, first saddle on ridge SSW of Mt. Mellenthin, Mancos Shale outcrop, 12,000 ft, 28 Jul 1984, *Tuhy 1847* (BRY).

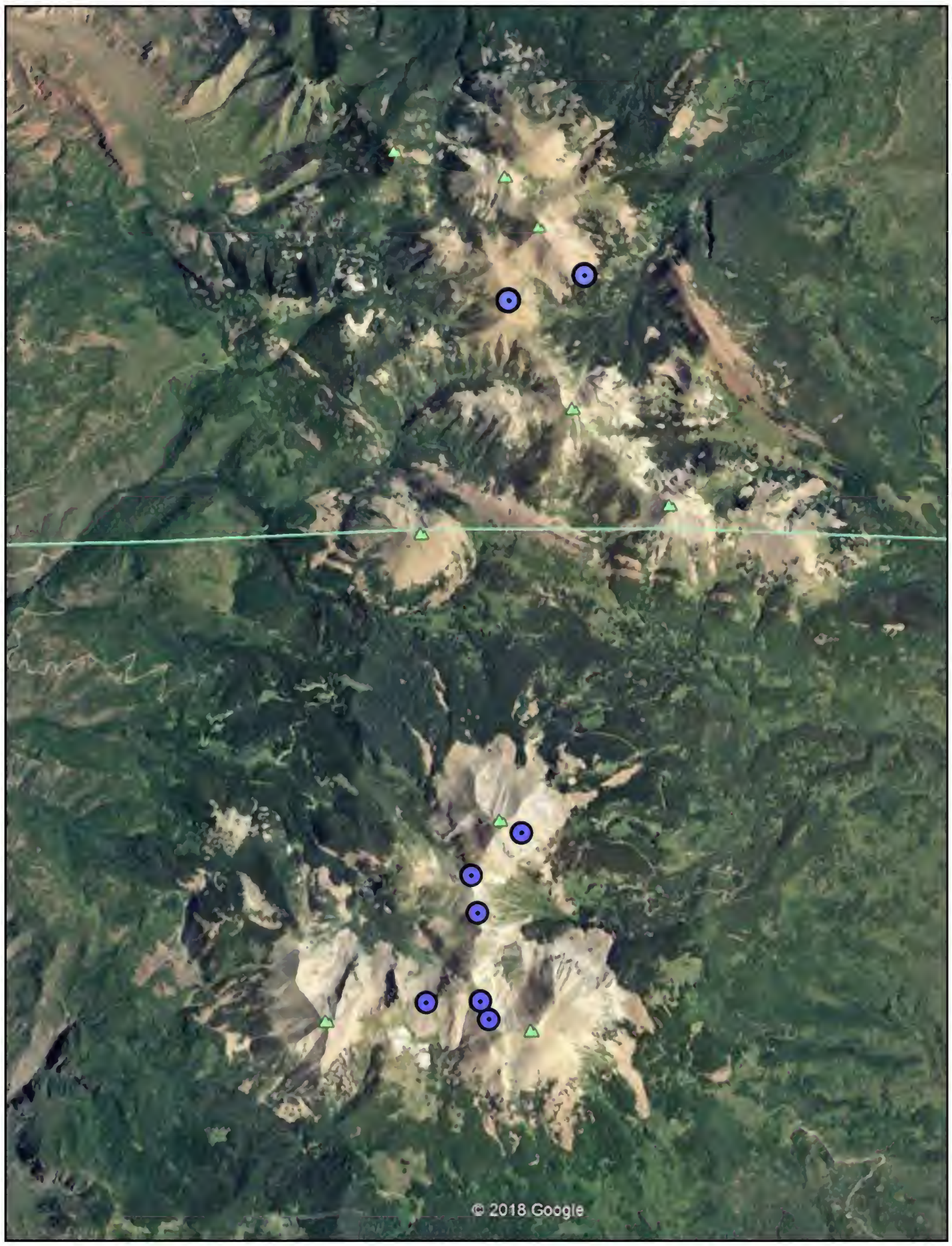

Figure 2. Distribution of *Senecio inexpectatus* in the La Sal Mountains of east-central Utah, based on collections cited in the text. Collections from this area in databases as *S. fremontii* var. *blitoides* are misidentified — all plants of *S. fremontii* sensu lato in the La Sals are *S. inexpectatus*. Base map from Google Earth; tiny green triangles are named peaks; the horizontal green line is the county line between San Juan County (south) and Grand County (north).

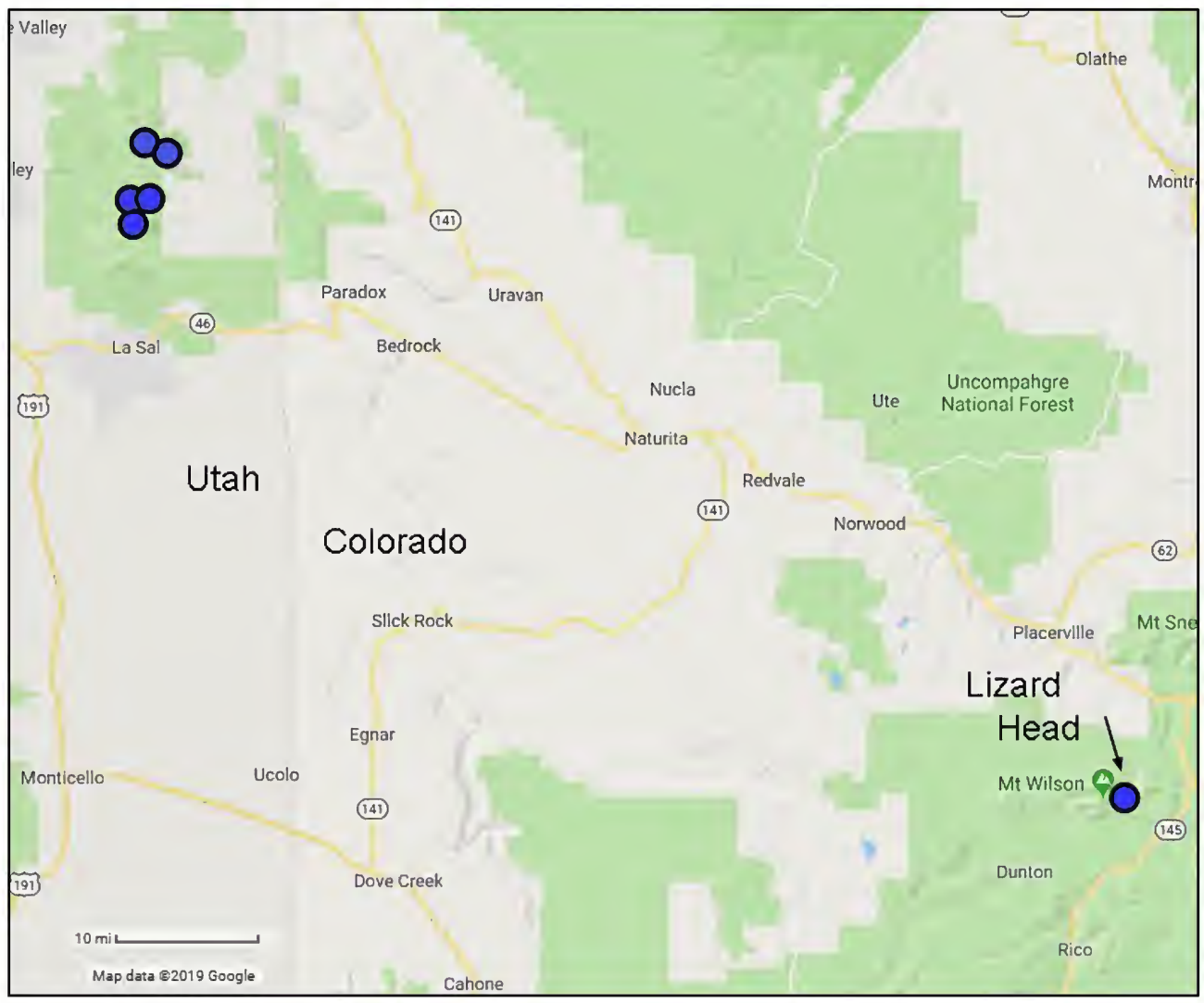

Figure 3. Distribution of *Senecio inexpectatus* in Utah and Colorado. The Colorado locality is in the San Juan National Forest near Lizard Head Peak — in the San Miguel Mountains of the San Juan Range. See Figure 1 for perspective.

Figure 4. Population and habitat of *Senecio inexpectatus* on Manco Shale along Cross Mountain Trail, Dolores Co., Colorado. Photo by Al Schneider, 8 Aug 2007, with Betty Schneider looking toward Lizard Head Peak.

Figure 5. *Senecio inexpectatus*, Dolores Co., Colorado, along Cross Mountain Trail near Lizard Head Peak. Photo by Al Schneider, 8 Aug 2007.

Figure 6. *Senecio inexpectatus*, holotype, San Juan, Co. Utah. *Cronquist & Holmgren 9464* (NY).

Figure 7. *Senecio inexpectatus*, Dolores Co., Colorado. *Schneider s.n.* (COLO).

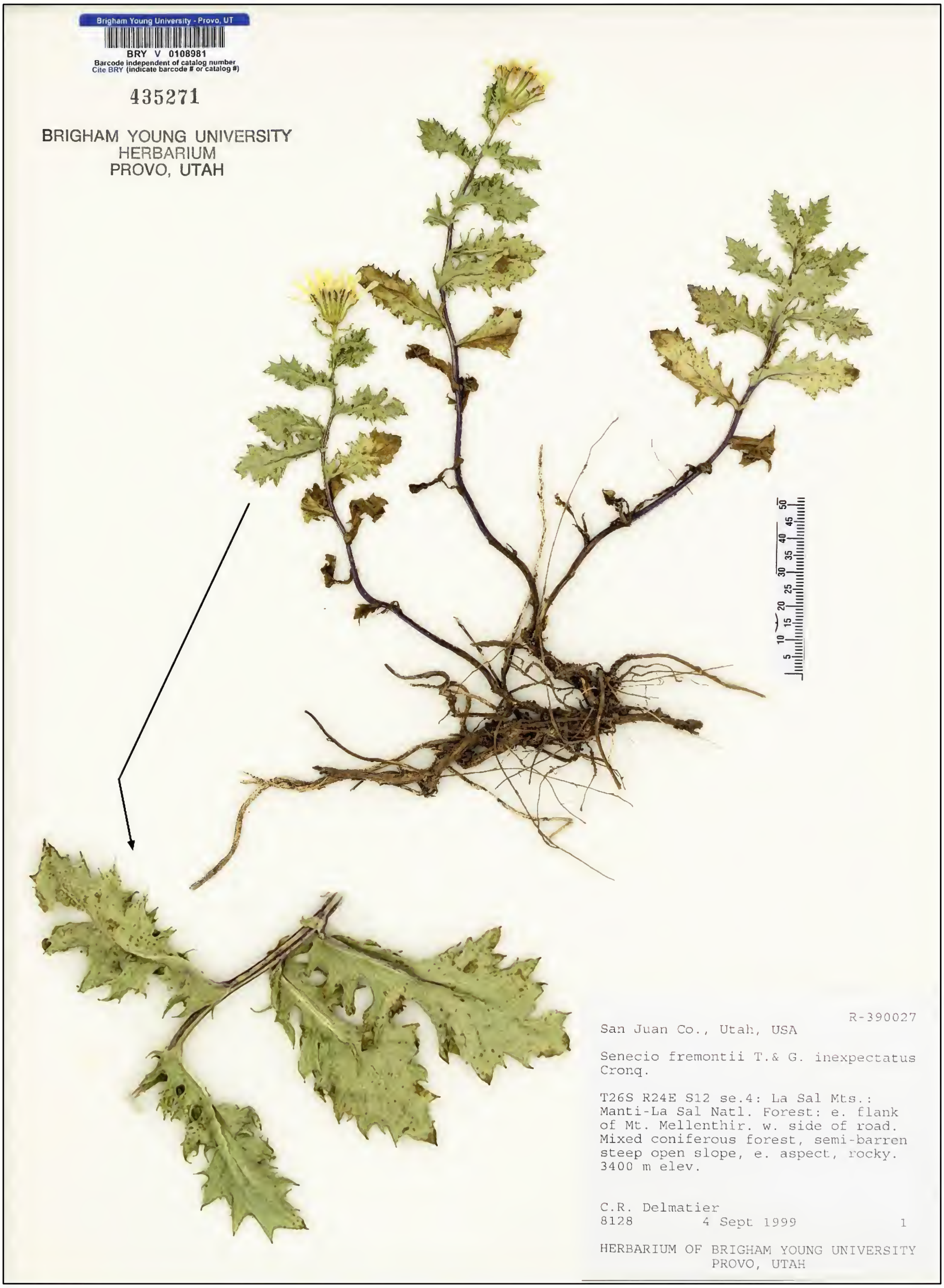

Figure 8. *Senecio inexpectatus*, San Juan Co., Utah. *Delmatier 8128* (BRY).

Figure 9. *Senecio inexpectatus*, San Juan Co., Utah. *Franklin 2039* (BRY).

2. SENECIO BLITOIDES Greene, Pittonia 4: 123. 1900. *Senecio fremontii* var. *blitoides* (Greene) Cronq. in Hitchcock et al., Vasc. Pl. Pacif. N.W. 5: 290. 1955. *Senecio fremontii* subsp. *blitoides* (Greene) W.A. Weber, Phytologia 53: 190. 1983. **TYPE**: **Colorado**. [Lake Co.]: Mt. Elbert near Leadville, near snowbanks, growing in dense clumps, 12,000 ft, 28 Aug 1899, *H.T. Holm 445* (holotype: NDG image; isotypes: F, WIS). The WIS sheet, with Holm's handwritten label, has "No. 445" — the NDG and F labels have no number.

Senecio carthamoides Greene, Pittonia 4: 122. 1900. **TYPE**: **Colorado**. [Saguache Co.]: Little Ouray Mtn., 3 Sep 1896, *E.L. Greene s.n.* (holotype: NDG image).

Senecio invenustus Greene, Pittonia 4: 124. 1900. **TYPE**: **Colorado**. [Archeluta Co.]: Near Pagosa Peak, 12,000 ft, 23 Aug 1899, *C.F. Baker s.n.* (holotype: NDG image; isotypes: NY, RM, US).

These three names by Greene of *Senecio* at generic rank were published 10 Jan 1900; "blitoides" has been the epithet generally used to refer to the Colorado/southern Rocky Mountain plants.

The main population system of *Senecio blitoides* is in Colorado, with extensions into adjacent Wyoming and New Mexico; a collection from a disjunct locality in Duchesne Co., Utah (Fig. 1), also is unambiguously *S. blitoides*; typical *S. fremontii* also occurs in Duchesne Co. Vouchers documenting both species in Duchesne Co. are cited here and photos are provided for contrast.

Senecio blitoides. Duchesne Co.: Uinta Mts., head of South Fork Rock Creek, 2.5 mi S of Grandaddy Lake, head of cirque basin, limestone talus slopes, 11,000 ft, 16 Aug 1994, *Huber & Goodrich 2277* (BRY, UTC). Figure 19. **Senecio fremontii**. Duchesne Co.: Uintah Mts., Swift Creek drainage, just N of Farmers Lake, alpine talus slope, 11,100 ft, 20 Aug 1992, *Goodrich 23977* (BRY). Fig. 29.

The geographic range of *Senecio blitoides* is discrete and disconnected from that of *S. fremontii* — there is no opportunity for gene flow between the two, except in the Utah locality, where both occur in typical form. The series below of herbarium specimens shows the range of morphological variation in each species: *S. blitoides*, Figs. (10-18) and *S. fremontii*, Figs. (19-31).

3. SENECIO FREMONTII Torr. & Gray, Fl. N. Amer. 2(3): 445. 1843. *Senecio ductoris* Piper, Contr. U.S. Natl. Herb. 11: 601. 1906 [intended replacement name for *S. fremontii* because of prior *Senecio filifolius* var. *fremontii* Torr. & Gray]. **Type**: **Wyoming**. [Sublette Co.]: Wind River Mts., 15 Aug 1842, *Lieut.* [J.C.] *Fremont s.n.* (holotype: GH image). Protologue: "On the Wind River Chain of the Rocky Mountains, just below the limits of perpetual snow, *Lieut. Fremont!* Aug."

Senecio fremontii var. *occidentalis* A. Gray in Brewer et al., Bot. California 1: 618. 1876. *Senecio occidentalis* (A. Gray) Greene, Pittonia 4: 122. 1900 [19 Jan]; not *S. occidentalis* (A. Gray) Rydb., Mem. New York Bot. Gard. 1: 437. 1900 [15 Feb]. *Senecio fremontii* subsp. *occidentalis* (A. Gray) G.W. Douglas & Ruyle-Dougl., Canad. J. Bot. 56: 1710. 1978 [nom. illeg., basionym not cited]. **Lectotype** (Cronquist 1994, p. 171): **California**. [Tulare/Inyo Co.]: Mt. Whitney, 12,000 ft, Sep 1875, *J.T. Rothrock 388* (GH image). Protologue: "Sierra Nevada, on Mount Whitney at 12,000 feet, and S. Fork of Kern River down to 9,8000 feet, Rothrock in Wheeler's Exped., 1875." Three Rothrock collections referred to by Gray are mounted on the same sheet (***349***–S Fork Kern River (Fig. 17), ***380***–S Fork Kern River, and ***388***–Mt. Whitney); Rothrock (1878) also cited all three collections. Barkeley annotated the GH sheet in 1973 as "holotype" with a centrally placed label, without indicating which collection he was referring to. Cronquist (1994) noted that "*Rothrock 388* … is regarded as the type, at GH!".

Senecio occidentalis (A. Gray) Greene var. *rotundatus* Rydb., Mem. New York Bot. Gard. 1: 438. 1900. **Lectotype** (designated here): **Idaho**. [Fremont Co.]: Mt. Chauvet, 10,000 ft, 29 Jul 1897, *P.A. Rydberg & E.A. Bessey 5268* (NY image). The Rydberg and Bessey sheet is annotated as the holotype, but Rydberg's protologue cited two collections — the other is "Wyoming [Teton Co.]: Breccia Peak, 1897, *Tweedy 589.*"

Figure 10. *Senecio blitoides*, isotype, Lake Co., Colorado. *Holm 445* (F).

Figure 11. *Senecio blitoides*, Conejos Co., Colorado. *Douglas 1367* (COCO).

Figure 12. *Senecio blitoides*, Gunnison Co., Colorado. *Russell 28.21* (ASU).

Figure 13. *Senecio blitoides*, Hinsdale Co., Colorado. *Dixon 5391* (ALAM).

Figure 14. *Senecio blitoides*, El Paso Co., Colorado. *Lath-House 1/2* (COCO). Large leaves, a populational variant as in the type of *S. carthamoides* from Saguache County.

Figure 15. *Senecio blitoides*, Boulder Co., Colorado. *Wolcott 6* (COLO).

Figure 16. *Senecio blitoides*, Hinsdale Co., Colorado. *Regensberg 1917* (KHD).

Figure 17. *Senecio blitoides*, El Paso Co., Colorado. *Headington & Blauvelt 71* (COCO).

Figure 18. *Senecio blitoides*, Clear Creek Co., Colorado. *Anderson 943* (KHD).

Figure 19. *Senecio blitoides*, Duchesne Co., Utah. *Huber & Goodrich 2277* (BRY). Disjunct from main population system of *S. blitoides* (see Fig. 1) but of characteristic morphology and distinct from *S. fremontii* in Duchesne Co. (see Fig. 29).

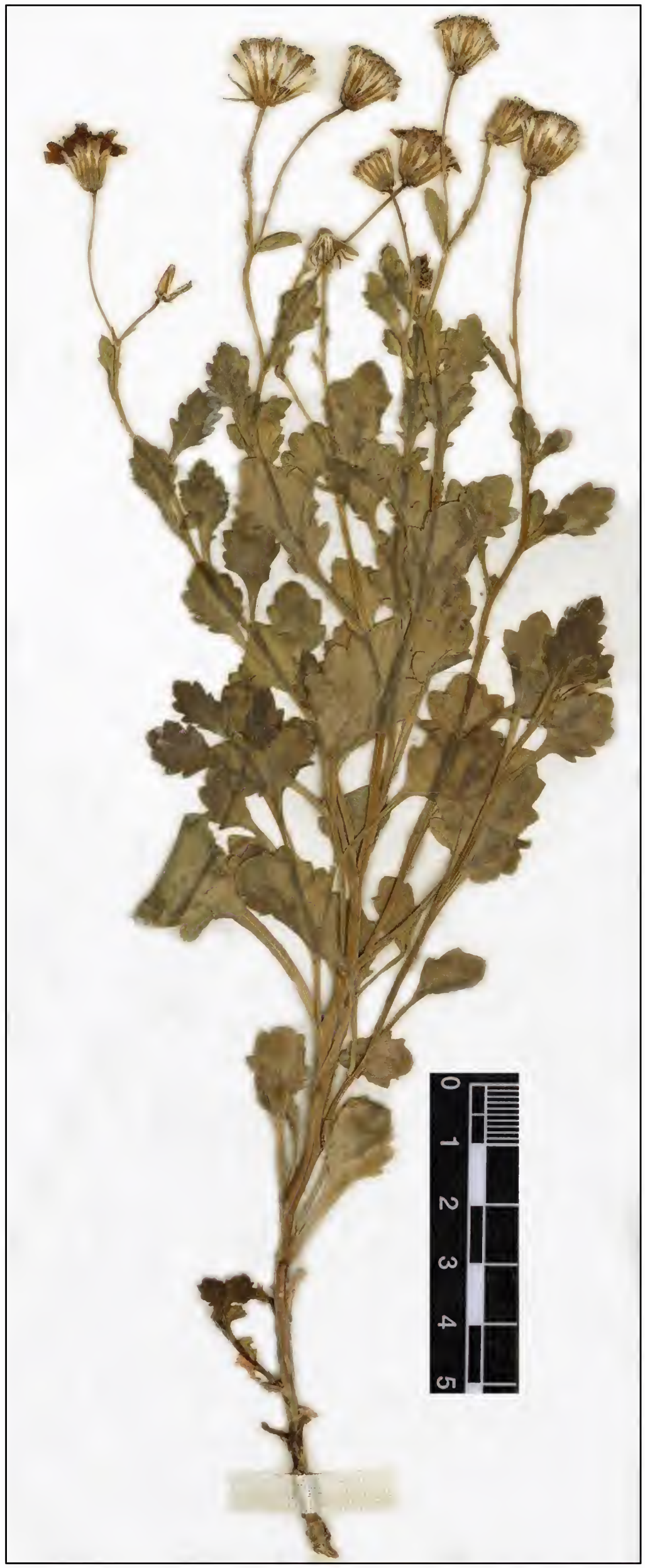

Figure 20. *Senecio fremontii*, syntype of *S. fremontii* var. *occidentalis* A. Gray. Tulare Co., California, South Fork of Kern River, 10,400 ft, Sep 1875, *Rothrock 349* (GH).

Figure 21. *Senecio fremontii*, Tulare Co., California. *Rice 493* (IND).

Figure 22. *Senecio fremontii*, Washoe Co., Nevada. *Tiehm 14,338* (RENO).

Figure 23. *Senecio fremontii*, Steens Mountain, Harney Co., Oregon. *Smith 7045* (WTU).

Figure 24. *Senecio fremontii*, Pierce Co., Washington. *Flett 3213* (WTU).

Figure 25. *Senecio fremontii*, Skagit Co., Washington. *Zika 18884* (WTU).

Figure 26. *Senecio fremontii*, Chelan Co., Washington. *Thompson 12,616a* (WTU).

Figure 27. *Senecio fremontii*, Tooele Co., Utah. *Neese 9666* (BRY).

Figure 28. *Senecio fremontii*, Box Elder Co., Utah. *Holmgren 8179* (NY).

Figure 29. *Senecio fremontii*, Duchesne Co., Utah. *Goodrich 23977* (RENO). See Figure 19 for a collection of *S. blitoides* from Duchesne Co.

Figure 30. *Senecio fremontii*, Summit Co., Utah. *Goodrich 26,111* (BRY).

Figure 31. *Senecio fremontii*, Park Co., Wyoming. *Jones 38,648* (COLO).

Figure 32. *Senecio fremontii*, Johnson Co., Wyoming. *Fonken 903* (COLO).

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SYMPHYOTRICHUM ESTESII, A NEW SPECIES OF VIRGULOID ASTER FROM TENNESSEE (ASTERACEAE: ASTEREAE)

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ABSTRACT

A new species of virguloid aster is described from collections from May Prairie, Coffee Co., Tennessee. The species was first discovered by Dwayne Estes, for whom the species is named, and is only known from the type locality in a single hydroxeric oak savanna remnant. **Symphyotrichum estesii** Semple, **sp. nov.**, is similar to *S. fontinale* but has white rays, somewhat smaller involucres lacking obvious anthocyanin, smaller floral parts, and longer peduncles with numerous small bracts. It is determined from meiotic cells to have a chromosome number of $2n$ = ca. 20_{II}. The new species is similar to *S. fontinale* and less so to *S. oblongifolium*, *S. grandiflorum* and *S. ericoides*.

In October 2008, Dwayne Estes observed a fruiting specimen of an unknown species of *Symphyotrichum* while visiting May Prairie State Natural Area, Coffee Co., Tennessee. Estes, who at the time was coauthoring the *Fifth Checklist of Tennessee Vascular Plants* (Wofford et al. 2009), realized that it was not a species then known as part of the Tennessee flora. Because the plant was past anthesis, he was not able to make a conclusive identification. In October 2010, Estes visited May Prairie again and found the plants to be in full flower — he photographed the plants and collected specimens (*Estes 11799*, APSC). Estes sent digital photographs to multiple botanists including J.C.S., who immediately recognized it as a likely new species, similar to *S. fontinale* (Alex.) Nesom (Brouillet et al. 2006). The site was visited again by the author, Mason Brock, Julian Campbell, Todd Crabtree, Dwayne Estes, and Ed Schilling, on 12 September 2012 (Figs. 1-2). The species is described here for the first time as ***Symphyotrichum estesii***, named in honor of its discoverer Dwayne Estes, a native of south-central Tennessee, professor of biology and herbarium director at Austin Peay State University, and executive director and co-founder of the Southeastern Grasslands Initiative (2019).

SYMPHYOTRICHUM ESTESII Semple, **sp. nov.** **TYPE**: **USA**. **Tennessee**. Coffee Co.: SE of Manchester, E of US-41, just E of 35° 26' 56.4" N, 86° 01' 55.5" W, May Prairie, scattered over large wet prairie glade, 326 m, $2n$ = ca. 20_{II}, 12 Sep 2012, *J.C. Semple, D. Estes, E. Schilling, T. Crabtree, J. Campbell, & M. Brock 11858* (holotype: MO; isotypes: APSC, BRIT, GH, NCU, NY, TENN, US, WAT in MT; all to be distributed; Thiers, continuously updated; Figs. 2-5).

Similar to *Symphyotrichum fontinale* (Fig. 6) but rays white at anthesis (never pale pink to bluish or violet), somewhat smaller heads (involucres 5–6.4 mm vs. 6–7.6 mm) and floral parts, and peduncles green (vs. anthocyanotic) with numerous congested small green bracts (vs. anthocyanotic bracts).

Perennials, colonial from long rhizomes. Stems 30–85 cm, solitary or several, erect (green with some light to reddish brown, somewhat striate, proximally moderately to densely hispidulo-strigillose, distally moderately to densely hispidulo-strigillose, sometimes sparsely stipitate-glandular. Leaves green, firm, margins sparsely serrate distally to entire, faces sparsely to densely short strigoso-scabrous, hairs usually denser and longer on abaxial veins, sometimes sparsely stipitate-glandular, usually curving upward from patent base; basal rosettes at base of stem absent at flowering; lower stem leaves oblanceolate, 50–66 × 6–9 mm, bases attenuate, margins entire to distally serrate, short scabrous, apices obtuse, short-mucronate; lower cauline often withering by flowering, sessile, blades

Figure 1. May Prairie, Coffee Co., Tennessee 12 September 2012. **A.** Dwayne Estes and *Symphyotrichum estesii*. **B.** Central portion of prairie; from left to right: Todd Crabtree, D. Estes, Mason Brock, Ed Schilling, J.C. Semple (Photograph by Julian Campbell). **C.** Northeast corner of prairie; from left to right: E. Schilling, D. Estes, T. Crabtree.

Figure 2. Holotype of *Symphyotrichum estesii, Semple et al. 10857* (MO, unmounted to be distributed).

Figure 3. Details of types of *Symphyotrichum estesii*, *Semple et al. 11857*: stems and leaves. **A.** Rhizomes and basal stem (BRIT). **B.** Lower stem (MO). **C-D.** Mid stems (WAT, GH). **E-F.** Lower stem leaf, abaxial surface (WAT in MT). **G.** Lower mid stem leaves (TENN). **H.** Mid stem leaf, abaxial surface (GH). **I.** Upper stem leaves (BRIT). **J.** Upper stem leaf, abaxial surface (BRIT). Scale bar = 1 mm in A-D, J; = 1 cm in E-I.

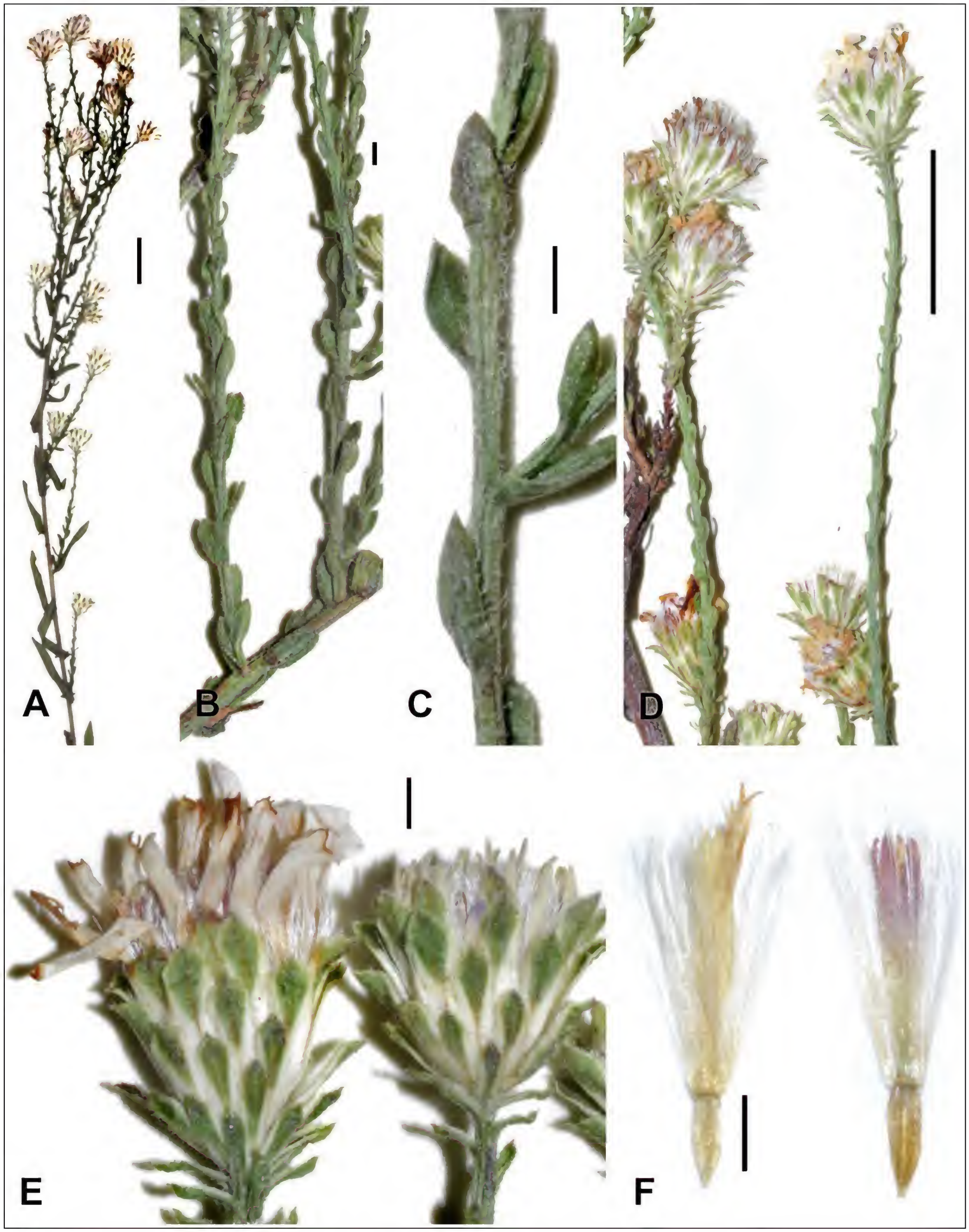

Figure 4. Details of types of *Symphyotrichum estesii*: floral traits. **A.** Small inflorescence with ascending branches (APSC). **B.** Peduncles (MO). **C.** Peduncle bracts (WAT). **D.** Heads and peduncles (APSC). **E.** Heads (APSC). **F.** Disc florets, flowering and post anthesis (MO). Scale bar = 1 cm in A, D; = 1 mm in B-C and E-F.

Figure 5. *Symphyotrichum estesii*: May Prairie, Coffee Co., Tennessee. **A.** Shoot. **B.** Rhizomes and stem. **C.** Ray and disc florets. **D.** Heads and peduncles.

oblanceolate to linear oblanceolate, 32–68 × 3–11 mm, margins distally shallowly serrate to entire, scabrellous, apices spinulose-mucronate; mid stem leaves sessile, blades lanceolate or oblanceolate to oblong-lanceolate, 18–45 × 2–7 mm, reduced distally and becoming bractlike in inflorescence, bases rounded, margins scabrous, apices acute to white-mucronulate or -subspinulose, faces sometimes shiny, minutely gland-dotted; branch leaves much reduced, 1–7 × 0.5–3 mm. Heads (5–50) in wide to narrow, paniculiform arrays, branches ascending to widely spreading, densely small-leaved. Peduncles ascending, rarely divergent, 1–5 cm, sparsely to densely strigoso-hirsute, sparsely stipitate-glandular, bracts dense, curving upward from patent base, narrowly oblong to broadly oblanceolate, mostly 1.5–2.5(–5) × 0.5–1(–2.5) mm, spinulose-mucronate, sparsely to moderately strigilloso-scabrous, sparsely minutely stipitate-glandular, grading into phyllaries. Involucres cylindro-campanulate, 5–6.4 mm. Phyllaries in 4–5 series (appressed), oblong or oblanceolate, unequal, bases indurate, glabrate to sparsely strigose, sparsely minutely stipitate-glandular, not anthocyanotic, margins hyaline, scarious, ciliate or ciliolate, green zones narrowly oblanceolate to obrhombic (inner), apices erect, acute to acuminate, mucronulate to apiculate (inner). Rays 9–17, laminae 2–4.5 × 0.6–1.2 mm, white. Disc florets 12–28; corollas yellow turning reddish purple to brownish, 3.6–5 mm, lobes triangular, 0.4–0.7 mm. Cypselae tan, obovoid-fusiform, slightly compressed, 1.9–2.3 mm, 4–6-nerved, faces sparsely strigillose to glabrescent; pappi 4.5–5.5 mm, the longest inner very weakly clavate.

Flowering Aug-Nov. Prairie and oak savanna; of conservation concern.

Additional collections. **Tennessee**. Coffee Co.: May Prairie and surrounding woods, 2 Sep 1984, *Medley 11505-84* (APSC, digital image! posted on SERNEC Data Portal. 2019; originally identified as *Aster dumosus* L.); May Prairie Natural Area, in W half of open prairie, 19 Oct 2010, *Estes 11799* APSU; May Prairie, 11 Oct 2014, *Brock et al. 797* (APSC, digital image! posted on SERNEC Data Portal. 2019; as *Symphyotrichum* sp.). Estes (pers. comm.) indicates that two additional collections not seen via SERNEC by the author are also likely specimens of *S. estesii* — a E. Quaterman collection (VDB?) and H. DeSelm collection (TENN?).

The collections of *Symphyotrichum estesii* have previously been misidentified as one of several aster species, including *S. dumosum*, *S. ericoides*, and possibly *S. pratense*. In aspect, with its white rays and habit, it is most likely to be confused with *S. dumosum* but can readily be distinguished by its erect-ascending cauline leaves (vs. spreading-descending), difference in vestiture, etc. From *S. ericoides* it is readily separated by phyllaries lacking a spinulose tip. *Symphyotrichum pratense* has purple rays, larger heads, and different vestiture but is somewhat similar in its sparingly branched habit with ascending branches.

Symphyotrichum estesii is closely similar to *S. fontinale*. In addition to features of difference noted in the diagnosis, *S. estesii* is disjunct from the range of *S. fontinale*. The latter is endemic to Florida and the bottom tier of counties in Georgia.

Symphyotrichum estesii shares stem, leaf, and inflorescence traits and stipitate-glands with *S. fontinale* (2*n*=50), which is native to Florida (Brouillet et al. 2006; Semple 2014), and less so with *S. oblongifolium* (2*n*=10, 20) of *S.* subg. *Virgulus* sect. *Grandiflori*, which also includes *S. campestre* (2*n*=10), *S. fendleri* (2*n*=10), *S. grandiflorum* (2*n*=60), *S. pygmaeum* (no count), and *S. yukonense* (2*n*=10).

The meiotic count or $2n$ = ca. 20_{II} is based on multiple pollen mother cells examined in diakinesis and metaphase I. No mitotic count confirmation was possible because the rootstocks did not transplant successfully to the greenhouse. The base number is $x = 5$; $2n = 40$ is octoploid.

Figure 6. *Symphyotrichum fontinale*: *Semple 11700* (WAT), Taylor Co., Florida. **A.** Shoots. **B.** Upper mid stem and leaves. **C.** Inflorescence branches. **D.** Florets. **E.** Heads and peduncles.

Symphyotrichum estesii is currently known only from May Prairie State Natural Area (SNA) in Coffee Co., Tennessee. May Prairie has long been known to Tennessee botanists as a unique unplowed grassland that harbors perhaps more rare species than any other site in the state, including many species that are disjunct from the longleaf pine savannas and wetlands of the Coastal Plain (Sorrie & Weakley 2001). Noss (2012), in *Forgotten Grasslands of the South*, points out the significance of May Prairie as one of the Mid-South's best remaining grasslands. The site is owned by the Tennessee Department of Environment and Conservation's Division of Natural Areas, which also manages the site with prescribed fire and periodic mowing. This region of Tennessee has been known as "The Barrens" for more than 200 years, a term given by early English-speaking settlers who visited the area in the late 1700s-early 1800s (DeSelm 1990, 1994).

Symphyotrichum estesii occupies a global range of less than 5 ha, consisting of portions of two prairie openings within the May Prairie SNA. It is rare and of conservation concern due to its geographically restricted range, but the one known population is being well managed on the natural area and appears to be stable. Additional searches by D. Estes in areas of suitable habitat on the nearby Arnold Air Force Base in 2011 did not turn up any additional populations (D. Estes, pers. comm.). More searches for this species are needed in the region and in other similar types of grassland habitats in the southeastern USA.

Symphyotrichum estesii is endemic to open, sunny, seasonally wet grasslands, specifically prairie-like openings among what historically was post oak savanna of the Eastern Highland Rim, part of the Interior Plateaus Ecoregion. These grasslands are associated with flat sites with acidic silt loam soils (of the Guthrie and Dickson soil series) underlain by a clay fragipan (Web Soil Survey 2019). These soils are hydroxeric, i.e., frequently waterlogged in winter and spring (with frequent surface ponding) and highly desiccated in late summer and fall, owing to the presence of the fragipan at a depth of 0.5-0.9 m. Tree ring studies by Stambaugh et al. (2016) show a fire record dating back to 1610 with a conservative fire return interval of 3.2-5.5 years, which along with grazing, would have been sufficient to maintain the area as a combination of oak savanna and prairie in pre-European settlement times (Estes et al. 2016). These grasslands are classified by NatureServe (2019) as part of the Eastern Highland Rim Prairie and Barrens Ecological System and by the Southeastern Grasslands Initiative (2019) as part of the Highland Rim Savanna community (Estes et al. 2016).

Within the prairie proper, *Symphyotrichum estesii* is common and abundant but is less so within the partially shaded adjacent oak woodlands, where it drops out almost entirely within a couple dozen meters from the prairie edge. In the prairie, it is associated with a rich diversity of native graminoids: *Andropogon gerardii*, *Calamagrostis coarctata*, *Carex meadii*, *Panicum virgatum*, *Rhynchospora chalarocephala*, *R. glomerata*, *Schizachyrium scoparium* var. *divergens*, and *Sorghastrum nutans*; forbs: *Agalinis decemloba*, *A. purpurea*, *Aletris farinosa*, *Asclepias hirtella*, *Baptisia aberrans*, *Castilleja coccinea*, *Coreopsis tripteris*, *Drosera brevifolia*, *Eryngium integrifolium*, *E. yuccifolium* var. *yuccifolium*, *Eupatorium hyssopifolium*, *E. leucolepis*, *E. pilosum*, *E. rotundifolium*, *Eurybia hemispherica*, *Euthamia leptocephala*, *Helianthus mollis*, *Lespedeza capitata*, *Liatris spicata*, *Oenothera tetragona* var. *sharpii*, *Packera crawfordii*, *Parthenium integrifolium*, *Polygala cruciata*, *Pycnanthemum muticum*, *P. tenuifolium*, *Rhexia mariana* var. *mariana*, *Rudbeckia palustris*, *Silphium mohrii*, *S. pinnatifidum*, *Sisyrinchium atlanticum*, *Solidago austrina*, *Symphyotrichum dumosum*, and *Tephrosia virginiana*. Some of the taxa listed above are endemic or nearly-endemic to the prairies and savannas of the Highland Rim and closely adjacent ecoregions, including *Helianthus eggertii*, *Oenothera tetragona* var. *sharpii*, *Silphium mohrii*, *S. pinnatifidum*, and *Solidago austrina*. The recently described *Stenanthium tennesseense* Sorrie & Weakley is also narrowly endemic to this same system of grasslands (Sorrie & Weakley 2017).

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ASPIDISTRA ELATIOR (RUSCACEAE) NEW FOR THE ARKANSAS FLORA

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ABSTRACT

Aspidistra elatior is reported here for the first occurrence outside of cultivation in Arkansas. Escaped plants of *A. elatior* are documented from Union County and were present as two colonies growing along the upper bank of a small stream in a highly disturbed, urban greenbelt in the city of El Dorado. This record of *A. elatior* marks the first occurrence of the genus *Aspidistra* in the state's naturalized flora and the fourth documented occurrence of this species outside of cultivation in the USA. Photographs of *A. elatior* in habitat and keys to identification of the genera of Ruscaceae currently known from the Arkansas flora are provided.

In 2019, two colonies of escaped plants of *Aspidistra elatior* Blume (cast-iron plant) were documented from Union County in Arkansas (Figs. 1–2). This genus and species previously have not been documented in the Arkansas flora outside of cultivation (Smith 1994; Arkansas Vascular Flora Committee 2006; Gentry et al. 2013). The escaped colonies of *A. elatior* occurred toward the top of a steep bank of a small stream in a highly disturbed, urban greenbelt within the city of El Dorado, Arkansas. Each colony consisted of multiple plants/clones. Much of the greenbelt is surrounded by residential areas, with homesites bordering the areas where the *A. elatior* plants occurred. No cultivated plants of *A. elatior* were observed in the vicinity of the escaped plants. Although their origin is unknown, establishment is presumed to be via *A. elatior* plants discarded as horticultural waste or from propagules (plants, rhizome segments, or seeds) distributed to and subsequently deposited at the sites by stream water. It also is possible that one or both colonies may have originated from plants persisting from cultivation practices; however, no obvious evidence of prior cultivation was observed. Establishment and spread of plants within the colonies appeared to be mostly vegetative by rhizomatous offsets; one plant in one of the colonies had a single, immature fruit (Fig. 2); hence, some spread via seeds also is plausible.

Figure 1. (A–B) *Aspidistra elatior* escaped in Union Co., Arkansas. Both colonies of plants shown were present along a stream in a highly disturbed riparian zone of an urban greenbelt. Plants in A and B were separated by several meters.

Figure 2. (A–B) *Aspidistra elatior* escaped in Union Co., Arkansas. A. Colony (same as Fig. 1A) with fruit-bearing plant of *A. elatior* — this plant was at the lower edge of the colony (downslope and closest to the stream — indicated by the yellow arrow); it was the only plant observed with reproductive structures. B. Close-up view of fruit.

Voucher specimens. **Arkansas.** Union Co.: El Dorado, W/NW of intersection of Briarwood Dr. and Crestwood Dr., two colonies of escaped plants at top of steep stream bank in highly disturbed, urban greenbelt and riparian zone, each colony consisting of numerous plants/clones from rhizomatous offsets, one plant/clone with fruit, 31 Aug 2019, *Serviss 8701A, 8701B* (HEND).

Aspidistra elatior is a rhizomatous perennial that probably is native to Japan (Liang & Tamura 2000). It sometimes is cultivated in the USA and elsewhere as an accent or border plant because of its evergreen habit and ease of cultivation — *A. elatior* is tolerant of a wide range of conditions, including low light and poor soils, and may persist even under neglect (Bailey & Bailey 1976). *Aspidistra elatior* previously only has been documented in the USA from Alabama, Florida, and South Carolina (Payne 2010; Barger et al. 2012; Kartesz 2015; Franck et al. 2016; Keener et al. 2019), making our record, apparently, only the fourth documented occurrence of this species outside of cultivation in the USA. *Aspidistra* was not included in the Flora of North America treatment for the Liliaceae (Utech 2002).

Based on the discovery of *Aspidistra elatior* in Arkansas, the Ruscaceae family currently is represented by five genera and nine species in the state — species of *Maianthemum* and *Polygonatum* are native; the remaining taxa in the family are non-native. Arkansas genera of Ruscaceae may be distinguished reliably using the following key (for keys and descriptions of the species of *Liriope* and *Ophiopogon* that are known from the Arkansas flora, see Serviss et al. 2016a and 2016b).

1. Plants caulescent with obvious aerial stems bearing leaves.

2. Inflorescences terminal; perianth segments separate ..... **Maianthemum**
2. Inflorescences axillary; perianth segments united ..... **Polygonatum**

1. Plants acaulescent without obvious aerial stems bearing leaves (the clustered leaf sheaths of *Convallaria* may appear as stems).

3. Leaves deciduous, 30 cm or less long and ca 2.5–7.6 cm wide; flowers pendulous, arranged in one-sided racemes; perianth white or rarely pink and broadly campanulate..... **Convallaria**
3. Leaves evergreen and leathery, at least some of them longer than 30 cm, or if less than 30 cm, also less than 2(–2.5) cm wide; flowers straight or recurved (in *Ophiopogon*), solitary and perianth purple to dark purple or rarely pink, or flowers in racemes and perianth purple, lavender, violet, pink, or white, and not campanulate.

4. Leaves wider than 5 cm, broadly elliptic to oblong-elliptic; flowers solitary ..... **Aspidistra**
4. Leaves less than 3 cm wide, lanceolate to linear; flowers in racemes.

5. Pedicels of flowers recurved; flowers perigynous or epigynous; fruits (sarcotestas) bright blue ..... **Ophiopogon**
5. Pedicels of flowers straight; flowers epigynous; fruits (sarcotestas) black to dark blackish-blue ..... **Liriope**

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NEW RECORDS IN THE HYACINTHACEAE FOR THE ARKANSAS FLORA

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ABSTRACT

Hyacinthoides × *massartiana*, *Hyacinthus orientalis*, and *Muscari armeniacum* are reported here for their first occurrences outside of cultivation in Arkansas. Escaped plants of *H.* × *massartiana* are documented from Ouachita and Pulaski counties, escaped plants of *H. orientalis* are documented from two locations in Clark County, and escaped plants of *M. armeniacum* are documented from Clark, Faulkner, and Hot Spring counties. The Pulaski County record of *H.* × *massartiana* possibly was persistent from cultivation. Photographs of all three taxa in habitat and keys to identification of the blue-flowered Hyacinthaceae species present in the Arkansas flora are included, along with notes on the family.

In 2019, records of escaped plants of *Hyacinthoides* × *massartiana* Geerinck (*H.* × *variabilis* P. D. Sell; hybrid bluebell) and *Hyacinthus orientalis* L. (hyacinth) were documented from Ouachita and Clark counties, respectively, in Arkansas. An additional record of *H.* × *massartiana* from Pulaski County is provided, although the specimen record is from 1975. These two taxa previously have not been documented in the state outside of cultivation (Arkansas Vascular Flora Committee 2006; Gentry et al. 2013), and this account provides the first documented occurrences of these species and genera in the Arkansas flora. Also in 2016 and 2019, escaped plants of *Muscari armeniacum* Leicht. ex Baker (garden grape hyacinth) were documented from Clark, Faulkner, and Hot Spring counties, providing the first documented occurrence of this species in Arkansas outside of cultivation.

Hyacinthoides × *massartiana*

Escaped plants of *Hyacinthoides* × *massartiana* were documented from a single location in Ouachita County (Figs. 1–3). These plants were present as a small population that consisted of dozens of individuals and small clusters of plants (the clusters probably produced through a combination of bulb offsets and seed production — Fig. 2) scattered over a semi-wooded slope and adjacent area at the base of the slope in disturbed woods. Most of the escaped plants were present at the edge and slightly into the woods at the base of the slope. Both blue and white-flowered forms were present. Establishment of the escaped population appeared to be accomplished via seeds and their associated spread by water and/or gravity from presumably once cultivated plants that were present upslope. The plants of *H.* × *massartiana* at the top of the slope were present in a semi-wooded portion of an adjacent property—these plants appeared to at least in part be persisting from prior cultivation and likely were the initial source of the escaped population.

Figure 1. *Hyacinthoides X massartiana* in Ouachita County, Arkansas. Both plants shown were escaped in highly disturbed woods at the base of a gradual slope. Plants shown in A and B were separated by several meters and occurred as part of a larger population consisting of dozens of *H. X massartiana* plants.

Figure 2. White-flowered form of *H. X massartiana* just within disturbed woods adjacent to the main population. Notice the well-developed fruits present on these plants (several other plants in the population also had fruits).

A 1975 record of *H. X massartiana* from Pulaski County is present in the LRU collection; however, it is unclear from the specimen data as to whether this plant was escaped or persistent from cultivation practices. It is included here because no mention of cultivation or a residential address is given in the specimen data, and it may represent an additional occurrence of this taxon from the Arkansas flora.

Voucher specimens. **Arkansas.** Ouachita Co.: Several escaped plants on slope and base of slope at edge and within disturbed woods near old homesite, plants with range of phenotypes in inflorescence and floral morphology, off Hwy 24, across 24 from storage buildings, 1/2 mi from Y-Mart at intersection of 4 and 24, Camden, 6 Apr 2019, *Serviss 8680* (HEND). Pulaski Co.: Maddox Rd., 3 mi E of Hwy 107, 18 Apr 1975, *M. Pierce 300* (LRU, HEND).

Hyacinthoides X massartiana is a naturally occurring, interspecific hybrid between *H. non-scripta* (L.) Chouard ex Rothm. (English bluebell) and *H. hispanica* (Mill.) Rothm. (Spanish bluebell) that is frequent in many areas of Europe, with or without the presence of the parental taxa (Heywood 1980; Stace 2010), even though, apparently, the natural ranges of the two parental taxa only slightly are sympatric (Grundmann et al. 2010). In Britain, *H. X massartiana* is by far the commonest of the three taxa in gardens, where many plants are misidentified as *H. hispanica*. There is circumstantial evidence that hybridization of the parental taxa takes place in Britain, but most wild (escaped or planted) hybrids were introduced as such (Stace et al. 2015; Stace, personal communication, 2019). In the USA, it is widespread in cultivation and well-naturalized in Washington state and probably elsewhere, occurring in the absence of either parent (McNeill 2002). Individuals of *H. X massartiana* show a range of intermediacy between the parents, and in particular, have slightly one-sided racemes, slightly recurved tepals, stamens that are variable in length, and bluish or whitish anthers (Sell & Murrell 1996). The escaped *H. X massartiana* plants discovered in Ouachita County showed a range of inflorescence and perianth morphology intermediate between the two parental species, with some plants favoring more so the inflorescence and perianth morphology of *H. non-scripta*. *Hyacinthoides X massartiana* previously only has been documented from North Carolina, Oregon, and Washington (McNeill 2002; Kartesz 2015; USDA, NRCS 2019), making our record, apparently, only the fourth documented occurrence of this taxon outside of cultivation in the USA.

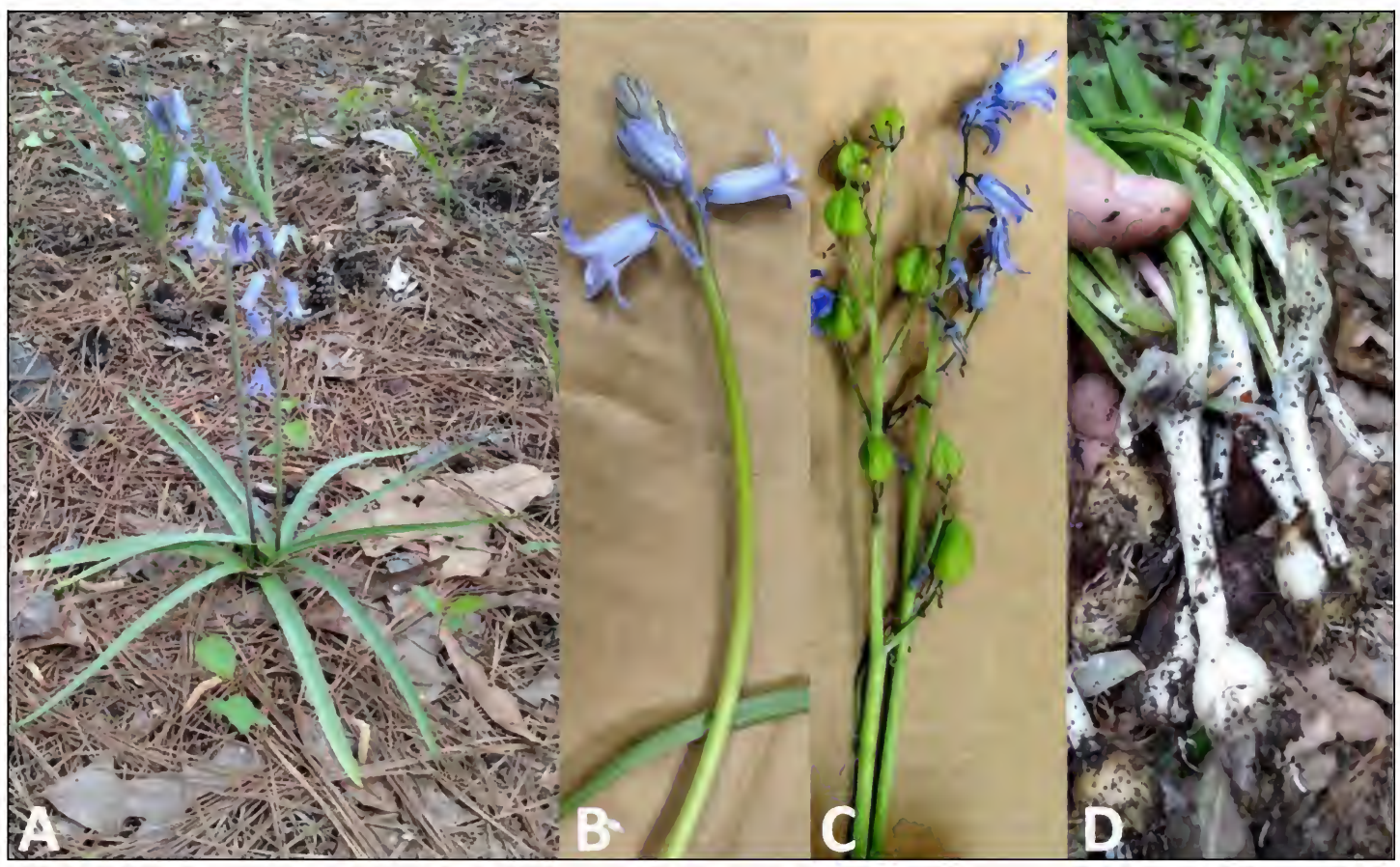

Figure 3. Inflorescences, flowers, fruits, and bulbs from escaped plants of *H. X massartiana* in Ouachita County, Arkansas. A–C. Some of the variation in inflorescence and perianth morphology among plants in the population. D. Bulbs of *H. X massartiana*.

Hyacinthus orientalis

Escaped plants of *Hyacinthus orientalis* were documented from two locations in Clark County, both with open, highly disturbed habitat (Figs. 4–6). Numerous escaped plants of *H. orientalis* were present at one of the two locations, and these plants ranged in development from small, isolated plants that evidently originated from seeds to small clusters, including immature and reproductively mature individuals, produced presumably through a combination of seed production and bulb offsets (Figs. 4–5). Escaped plants were scattered in distribution over a total area of several square meters that included ornamental beds and an adjacent lawn area. Establishment and spread of the escaped *H. orientalis* plants appeared primarily to be via seeds. The origin of the escaped plants presumably is from cultivated plants of the species that also were present at the location. *Hyacinthus orientalis* plants were observed with flowers, and later, with mature fruits. Some establishment via bulb offsets also was apparent.

Figure 4. *Hyacinthus orientalis* in Clark County, Arkansas. A–B. Two separate plants of *H. orientalis* escaped into the edge of a lawn. C. Fruits of *H. orientalis*.

The other location of escaped *H. orientalis* from Clark County had one large cluster of plants, with three smaller plants of various sizes in proximity that almost assuredly were produced via seeds from plants in the larger cluster (Fig. 6). These plants occurred at the edge of a small, wooded greenbelt on top of a steep slope at the dead end of a street in a residential area. The origin of the older plants in the larger cluster is unknown, but establishment from seeds, horticultural discards, or possibly even long-time persistence from cultivation is plausible (several plants of *Narcissus* × *incomparabilis* also were present). Although houses occur on either side of the street, no homesite existed at the location of the *H. orientalis* plants, as the area where the plants were present only is 1.5–2 meters wide before the edge of the adjacent slope.

Voucher specimens. **Arkansas.** Clark Co.: Numerous plants escaped in disturbed areas of property, including edge of lawn and adjacent ornamental beds — spreading and establishing from cultivated plants, W of Friendship exit off I–30, off Penn Rd. (NW of road), just N of intersection of Penn Rd. and Caney Rd., Friendship, 19 Mar 2019, *Serviss 8662* (HEND); one large group of plants and three smaller plants at dead end and edge of street and adjacent greenbelt, above steep slope, E end of Center St., about 1 block E of intersection of Center St. and 19th St., Arkadelphia, 19 Feb 2019, *Serviss 8653* (HEND).

Figure 5. *Hyacinthus orientalis* in Clark County from the same location as Fig. 4. A. Bulbs and offsets from *H. orientalis*; several small offsets may be seen to the left of the larger bulbs. B. Two small, escaped plants in highly disturbed habitat; these plants are a distance of at least 2–3 meters from the nearest *H. orientalis* plants.

Figure 6. *Hyacinthus orientalis* in Clark County from a different location than the plants shown in Figs. 4–5. A. Cluster of plants in narrow, highly disturbed area at end of street (no homesite present), which is above a steep slope of a wooded greenbelt in the city of Arkadelphia; its origin is unknown. B. Small plant (one of three that were present in addition to the lager cluster) presumably produced via seeds from the plants shown in 6A. The plant in 6B is separated from the larger cluster by several centimeters.

Hyacinthus orientalis is native to southwestern Asia and is cultivated and naturalized in Mediterranean Europe (Heywood & Regueiro 1980). It was not included in the Liliaceae treatment for Flora of North America (Utech 2002); however, it has been documented outside of cultivation in a number of states in the USA (Kartesz 2015; USDA, NRCS 2019). *Hyacinthus orientalis* frequently is cultivated for its showy, fragrant flowers. Plants of *H. orientalis* encountered in cultivation often show a somewhat distinct morphology, with larger body size and denser inflorescences with more flowers, as compared to the plants documented as escaped in Arkansas.

Muscari armeniacum

In 2019, escaped plants of *Muscari armeniacum* were documented from Clark and Faulkner counties and in 2016 from Hot Spring County (Figs. 7–8). Escaped plants from Faulkner and Hot Spring counties were present in lawns, with additional plants present at the edge of adjacent disturbed woods at the Hot Spring County site. Multiple plants were present at all sites (it is possible, of course, that some of these plants were persistent from cultivation practices; however, a number clearly were escaped). Spread via both seeds and bulblets appeared evident. These records represent the first documented occurrence of *M. armeniacum* in the Arkansas flora outside of cultivation. *Muscari armeniacum* was not included in Smith (1994), Arkansas Vascular Flora Committee (2006), Gentry et al. (2013), nor the Flora of North America treatment (only discussed) of the genus (Straley & Utech 2002). However, it is included in the Flora of the Southern and Mid-Atlantic States (Weakley 2015), where it is listed as persistent and/or escaped in lawns, old fields, suburban woods, and disturbed habitats, and it has been documented in the naturalized floras of California, Illinois, New York, and Ohio (Kartesz 2015; USDA, NRCS 2019).

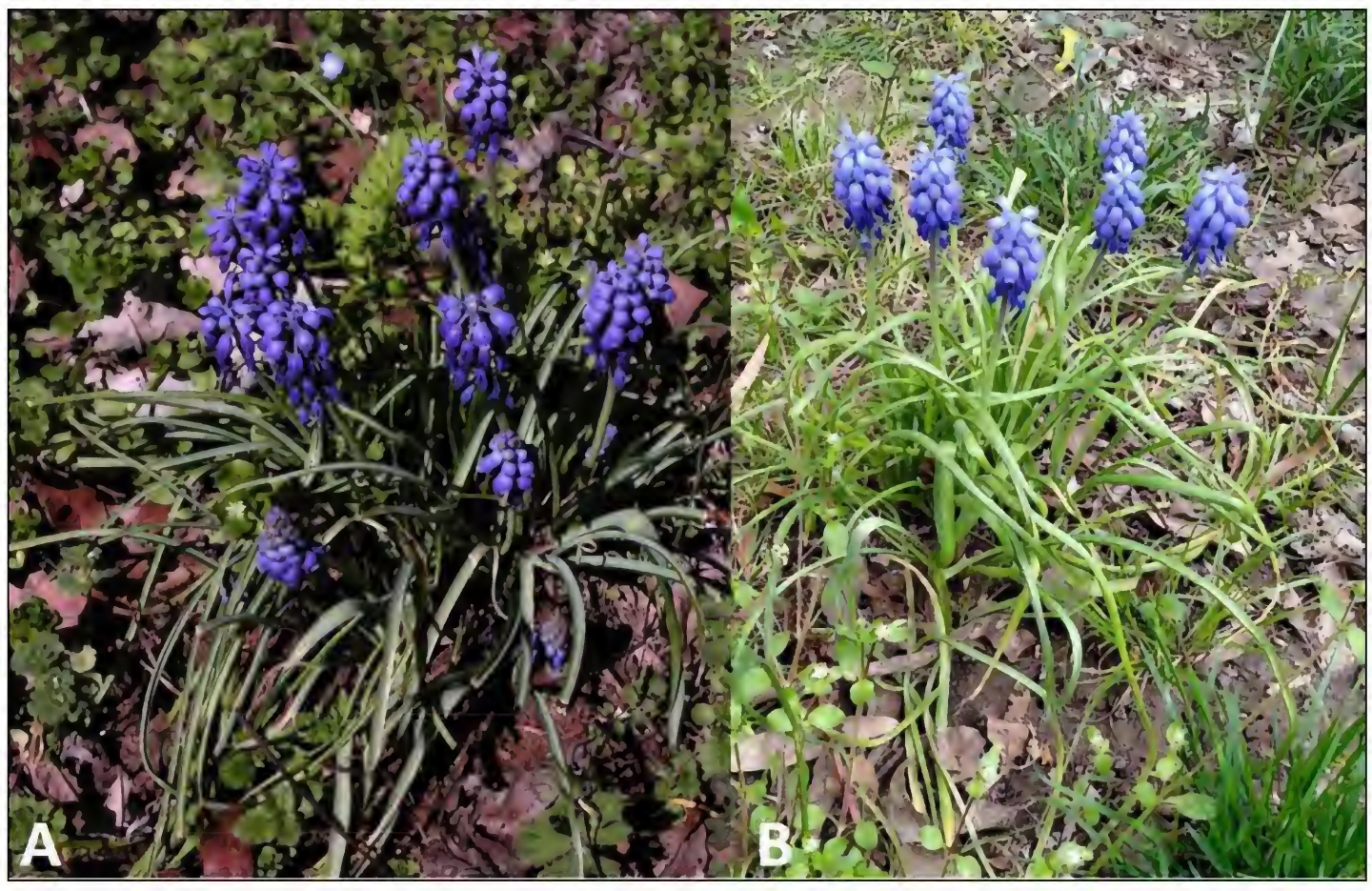

Figure 7. *Muscari armeniacum* plants escaped in Arkansas. A. Hot Spring County in 2016. B. Faulkner County in 2019.

Muscari neglectum Guss. ex. Ten. (starch grape hyacinth; Figs. 9–10), which closely resembles *M. armeniacum*, sometimes is cultivated in Arkansas and also is well naturalized in the state and elsewhere in the southeastern USA (Straley & Utech 2002; Gentry et al. 2013; Weakley 2015). The blue-flowered *Muscari* species naturalized in the USA are morphologically similar, and *M. armeniacum* and *M. neglectum* can be difficult to distinguish, especially from dried material (Straley & Utech 2002). The *M. armeniacum* plants documented from Arkansas appear to fit the descriptions of the species as provided by Davis and Stuart (1980) and Sell and Murrell (1996), and at

least some of the Arkansas material resembles the cultivar 'Christmas Pearl' based on the tinge of purple color to the flowers and shape of the inflorescences. In addition to the lighter blue flowers, some of the Faulkner County plants had seven leaves (per bulb), another trait attributed to *M. armeniacum*.

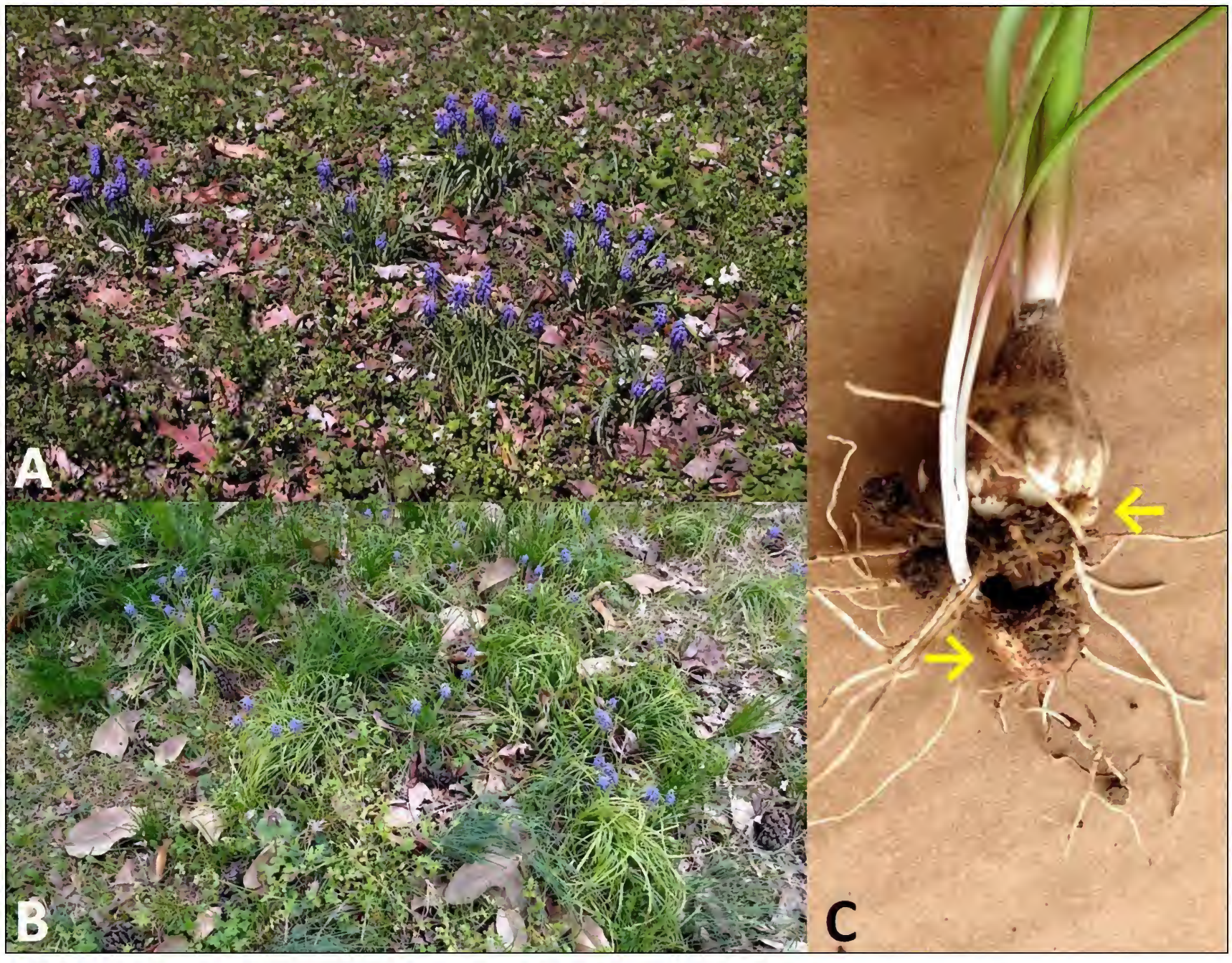

Figure 8. *Muscari armeniacum* escaped in Arkansas. A. Portion of escaped population in Hot Spring County. B. Portion of escaped population in Faulkner County (from one of two sites). C. Bulb showing two offsets (designated by yellow arrows) from one of the Faulkner County plants. All sites had multiple plants present. The Hot Spring County location, in addition to an unkempt lawn area, had multiple plants present at the edge of an adjacent, highly disturbed woods. The Faulkner County site shown in 8B had two to three groups of escaped plants in an unkempt lawn of a vacant homesite.

Voucher specimens. **Arkansas.** Clark Co.: Arkadelphia, many dozens of plants naturalized in open field/lawn area of vacant lot and edge of parking lot, off Pine St., directly NW of intersection of Pine St. and 10th St., W of service station, 23 Mar 2019, *Serviss 8663* (HEND). Faulkner Co.: Conway, several plants naturalized in lawn of yard and residence, off Clifton St., SW of intersection of Clifton St. and Mill St., 29 Mar 2019, *Serviss 8677* (HEND); Conway, several plants naturalized in weedy lawn of residence, at intersection of Mill St. and Ash St., NE of intersection, 29 Mar 2019, *Serviss 8674* (HEND). Hot Spring Co.: Magnet Cove, many plants naturalized in lawn area and edge of woods, weedy, off Smoke Ridge Rd., off Hwy 51, residence at 1979 Smoke Ridge Rd., 17 Mar 2016, *Serviss 8219* (HEND).

As a result of these records, the Hyacinthaceae family in the Arkansas flora is represented by four genera and eight species. Two species of *Muscari* (grape hyacinth) — *M. botryoides* (L.) Mill. and *M. neglectum*, along with *Ornithogalum umbellatum* L. (star of Bethlehem, bird's milk lily), are known from numerous counties in the state and the latter two species generally occur as weeds of open, disturbed areas — lawns, roadsides, edges of greenbelts, and other waste places. *Muscari* and

at least some *Ornithogalum* species (in Arkansas) apparently spread and naturalize via a combination of seeds and bulblets — *M. armeniacum*, *M. neglectum* (Fig. 9D), and *O. umbellatum* often prolifically produce bulblets from larger bulbs. Seeds and/or bulblets may be transported and dispersed by multiple factors, including water, redistribution of soil, or anthropogenic means. Based on our observations, both *H. × massartiana* and *H. orientalis* also appear to have the potential to be weedy under the correct conditions.

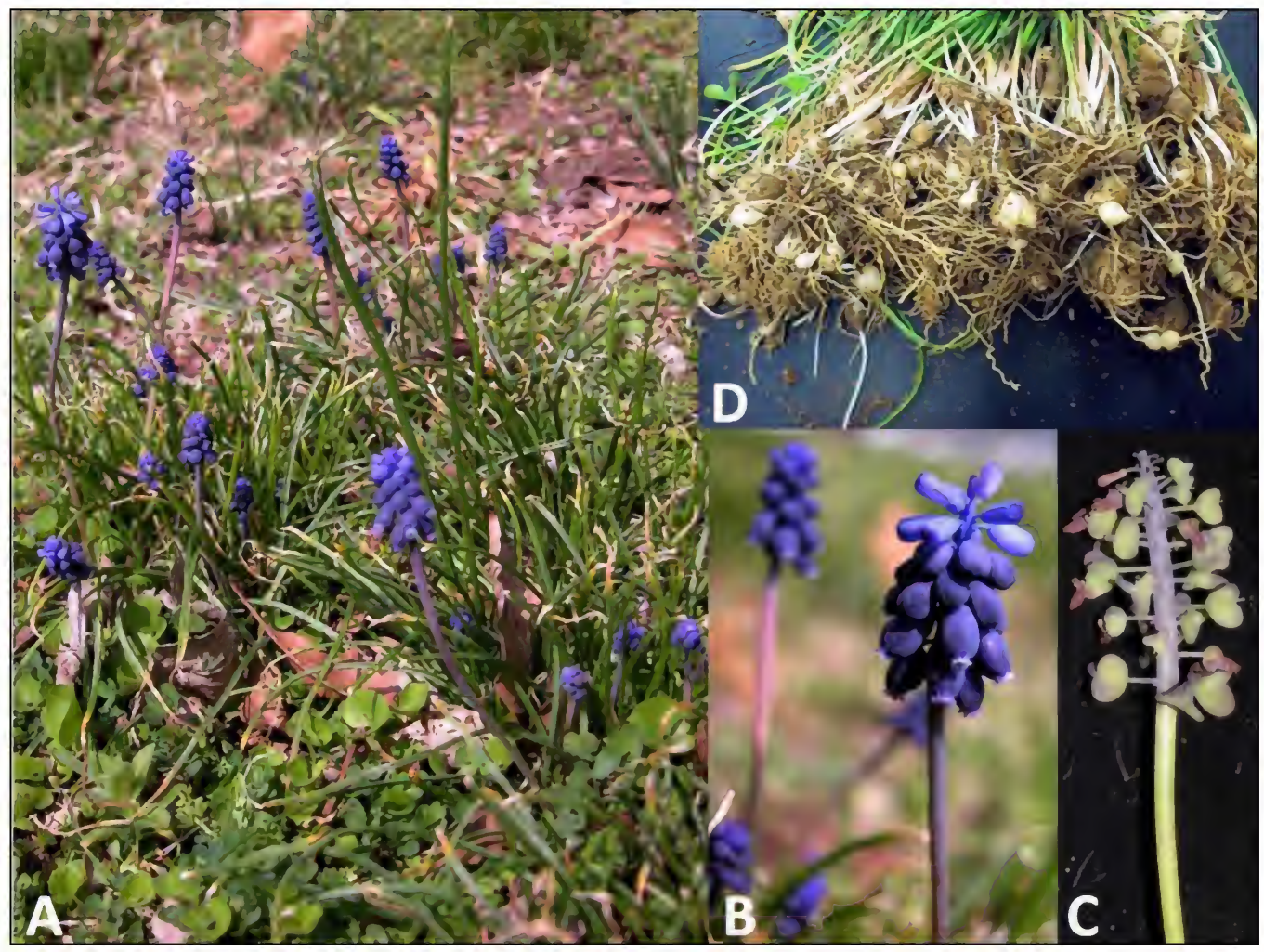

Figure 9. *Muscari neglectum* for comparison with *M. armeniacum*. A. Plant and habit. B. Flowers; notice the dark, almost blackish-blue coloration of the fertile flowers toward the base of the inflorescence — this characteristic helps to distinguish this species from *M. armeniacum*. C. Infructescence and mature fruits. D. Bulbs and bulblets; notice the prolific production of bulblets, which is typical for this species.

Figure 10. Naturalized population of *M. neglectum* in Clark Co., Arkansas. This population is large, consisting of hundreds of plants, and extends considerably beyond what is shown in the photograph.

The blue-flowered species of Hyacinthaceae currently documented from the Arkansas flora can be distinguished using the following key (modified from Davis & Stuart 1980; Sell & Murrell 1996; Straley & Utech 2002; Stace 2010; Weakley 2015).

1. Perianth segments united only basally, nearly separate ..... **Hyacinthoides x massartiana**
1. Perianth segments united one-half or more of their length.

2. Perianth segments united about one-half of their length; fruits more or less spherical ..... **Hyacinthus orientalis**
2. Perianth segments united nearly to apices; fruits sharply three-angled.

3. Perianth globose to ovoid, 1.3–1.5 times as long as wide, lobes strongly recurved; leaves 2–3(–4) in number, 3–8(–12) mm wide, erect, linear-oblanceolate or rarely linear, glaucous on upper surface; bulbs without offset ..... **Muscari botryoides**
3. Perianth ovoid, obovate, oblong-urceolate, or cylindrical, 2 or more times as long as wide, lobes usually erecto-patent; leaves (2–)3–7 in number, 1–5(–10) mm wide, recurved, generally linear, linear-lanceolate, or rarely linear-elliptic, glaucous or green; bulbs with or without offsets, but often with them.

4. Flowers 3.5–7.5 mm long, perianth of fertile flowers dark blue, dark violet-blue, or blackish-blue to blackish-purple; leaves 3–6 in number, linear to linear-lanceolate, canaliculate to involute, bright green, upper surface sometimes glaucous ..... **Muscari neglectum**
4. Flowers 3.5–5.5 mm long, perianth of fertile flowers bright blue or purplish-blue; leaves (2–)3–5(–7) in number, linear or linear-lanceolate, rarely linear-elliptical, often canaliculate, sometimes glaucous ..... **Muscari armeniacum**

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NEW COMBINATIONS AND NEW NAMES IN AMERICAN *CINNAGROSTIS*, *PEYRITSCHIA*, AND *DESCHAMPSIA*, AND THREE NEW GENERA: *GREENEOCHLOA*, *LAEGAARDIA* AND *PARAMOCHLOA* (POEAE, POACEAE)

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ABSTRACT

Based on morphological and molecular evidence we present new combinations or new names for 77 taxa of *Cinnagrostis*, seven taxa of *Deschampsia*, and 24 taxa of *Peyritschia*; and describe three new genera, **Greeneochloa** P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** (subtribe Echinopogoninae), **Paramochloa** P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** (subtribe Calothecinae), and **Laegaardia** P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** (subtribe Calothecinae) with two, two and one species, respectively. In addition to the 116 new taxonomic entities, we provide a key to the genera of American grasses presently or formerly treated in *Calamagrostis* or *Deyeuxia* and generic emendations for *Cinnagrostis* and *Peyritschia*.

RESUMEN

De acuerdo con evidencias de carácter morfológico y molecular se presentan nuevas combinaciones o nuevos nombres para 77 táxones de *Cinnagrostis,* siete táxones de *Deschampsia* y 24 táxones de *Peyritschia*, así como la descripción de tres nuevos géneros, **Greeneochloa** P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** (subtribu Echinopogoninae), **Paramochloa** P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** (subtribu Calothecinae) y **Laegaardia** P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** (subtribu Calothecinae) con dos, dos y una especie respectivamente. Además de las 116 nuevas entidades taxonómicas, proporcionamos una clave para los géneros de gramíneas americanas tratadas actual o anteriormente en *Calamagrostis* o *Deyeuxia* y enmendamos los genéros *Cinnagrostis* y *Peyritschia*.

In a large unpublished molecular DNA sequence study using four gene regions (ITS, *rpl32-trnL* spacer, *rps16-trnK* spacer, and *rps16* intron) we found most South American species of *Deyeuxia* Clarion ex P. Beauv. and *Calamagrostis* Adans., to align in a large clade excluding the type species of each of these genera (Peterson et al., in prep.). These results were largely corroborated by Saarela et al, (2010, 2017) in the study of Poeae R. Br. chloroplast group I where genera were split into Koeleriinae Asch. & Graebn. clade A (e.g. *Koeleria* Pers. and others) and Koeleriinae clade B (*Cinnagrostis* Griseb., *Peyritschia* E. Fourn., and others). We, therefore are resurrecting *Cinnagrostis* (Grisebach, 1874), a little known genus described from a single dichogamous species, *C. polygama*

Griseb., for the taxa in this South American clade. Sister to *Cinnagrostis* are Mexican and Central American species of *Trisetum* Pers., *Calamagrostis*, and *Peyritschia* that form the *Peyritschia* clade (Romaschenko et al. in prep.). Recent molecular phylogenetic studies confirmed that *Trisetum* s.l. is polyphyletic and now contains only two or three species (Soreng & Davis 2000; Quintanar et al. 2007; Saarela et al. 2017; Barberá et al. 2019). Finot et al. (2006) treated *Peyritschia* s.s. as having seven species but we are expanding it here to include 32 species. In our same unpublished molecular DNA study we found two species (*Greeneochloa* P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.**) of *Calamagrostis* from North America in a clade within the Echinopogoninae Soreng, and three species of *Calamagrostis/Deyeuxia* from South America in a clade within the Calothecinae Soreng that we treat here in *Laegaardia* P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** and *Paramochloa* P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** We also have molecular support to place four species and two varieties in *Deschampsia* P. Beauv. following the criteria used by Saarela et al. (2017).

The United States National Herbarium (US) in the Department of Botany, National Museum of Natural History, Smithsonian Institution, is in the process of rearranging the grass collection in a phylogenetic sequence following Soreng et al. (2017). To accommodate each grass genus in the family we have generated 781 G-numbers in our location poster called Systema Graminum (DOI:10.13140/RG.2.2.26027.34084). For using the US collection (or anyone else using our linear phylogenetic sequence) one must first look up the genus number and then proceed to the appropriate cabinet housing the specimens. G-numbers for the genera treated in this paper are: *Cinnagrostis* (210), *Deschampsia* (261), *Greeneochloa* (231B), *Laegaardia* (234E), *Paramochloa* (234C), and *Peyritschia* (216).

Based on our unpublished molecular DNA sequence phylogeny, and review of morphological characters on specimens and documented in primary protologues and secondary, we present new combinations or new names for 77 taxa of *Cinnagrostis*, seven taxa of *Deschampsia*, and 24 taxa of *Peyritschia*; and describe three new genera, *Greeneochloa, Paramochloa*, and *Laegaardia* with two, two and one species, respectively. In addition to the 116 new taxonomic entities, we provide a key to the genera of American grasses presently or formerly treated in *Calamagrostis* or *Deyeuxia*, and generic emendations for *Cinnagrostis* and *Peyritschia*. An asterisk (*) following the combination or name indicates we lack molecular evidence but based on morphology we feel confident in its placement.

TAXONOMY

CINNAGROSTIS Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 256–257, t. 2, f. 7. 1874, **gen. emend.**

TYPE: *Cinnagrostis polygama* Griseb. [≡ *Calamagrostis polygama* (Griseb.) Parodi ≡ *Deyeuxia polygama* (Griseb.) Parodi].

Description—Cespitose or rhizomatous perennials, a few stoloniferous. Culms 1−180 cm tall, generally erect, simple or branched; nodes glabrous or hairy. Leaf sheaths longer or shorter than the internodes, open, smooth or scabrous, glabrous or hairy; ligules usually ≤ 4.5 mm long [infrequently the longest 5 to 10(−15 mm)], membranous, apex truncate, rarely acuminate, usually scabrous or variously pubescent; leaf blades linear, straight or recurved, flat, convolute or conduplicate. Panicles terminal, lax or contracted, spiciform or subspiciform to globose, greenish, straw-colored, silver or gold. Spikelets 1−12 mm long, 1-flowered, laterally compressed, lanceolate to occasionally ovate; rachilla prologation usually hairy; disarticulation above the glumes; glumes 2, lanceolate, glabrous or scabrous, apex acute or acuminate, both exceeding the floret body; lower glumes 1-veined; upper glumes 1−3-veined, glabrous or scabrous along the median vein; lemmas membranous, glabrous or scabrous, usually smooth, 5-veined, apex acute, bifid, dentate or aristidate, usually awned dorsally from upper, middle or lower third, rarely mucronate; paleas usually slightly shorter than the lemma to as long, membranous, sometimes hyaline, 2-veined, 2-keeled; callus rounded, recurved or acute, hairy, rarely glabrous, the hairs shorter, as long or longer than the floret; stamens 3; ovary usually glabrous,

styles 2, stigmas feathery; lodicules 2, membranous, generally with 2 unequal lobes, glabrous or sometimes ciliate. Caryopses usually fusiform to oblong, sometimes laterally compressed, pericarp adherent, endosperm dry, pasty, or liquid. Basic chromosome number $x = 7$.

Distribution—Species of *Cinnagrostis* range throughout South America and extend to Central America, *C. rigescens* (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá reaching North America in Veracruz, Mexico (Tovar 1993; Rúgolo de Agrasar & Villavicencio 1998; Rúgolo de Agrasar 2006, 2012).

Comments—In a molecular phylogeny based on four gene regions (ITS, *rpl32-trnL* spacer, *rps16-trnK* spacer, and *rps16* intron) [henceforth referred to as Romaschenko et al. (in prep.)] the South American species of *Calamagrostis* and *Deyeuxia* form a clade sister to the Mexican and Central American species of *Trisetum, Calamagrostis*, and *Peyritschia* (most transferred below to *Peyritschia*), within the Koeleriinae clade B of the Aveninae J. Presl. Within the *Cinnagrostis* clade are two subclades, one containing species formerly placed in *Calamagrositis* sect. *Chamaecalamus* Pilg. [more recently placed in *Deyeuxia* sect. *Chamaecalamus* (Pilg.) Rúgolo & Villav.], which is sister to the remaining species in the genus (Pilger 1938; Rúgolo de Agrasar & Villavicencio 1995).

Cinnagrostis alba (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia alba* J. Presl, Reliq. Haenk. 1 (4–5): 248. 1830.

Cinnagrostis alba var. **breviaristata** (Rúgolo) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia alba* subsp. *breviaristata* Rúgolo, Darwiniana 44 (1): 146–147, f. 4C–D. 2006.

Cinnagrostis alba var. **tricholemma** (Roseng., B.R. Arrill. & Izag.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis alba* subsp. *tricholemma* Roseng., B.R. Arrill. & Izag., Gram. Urug. 27, f. 4. 1970.

Cinnagrostis boliviensis (Hack.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis boliviensis* Hack., Repert. Spec. Nov. Regni Veg. 6: 156. 1908.

Cinnagrostis breviaristata (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia breviaristata* Wedd., Bull. Soc. Bot. France 22: 177, 179. 1875.

Cinnagrostis brevifolia (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia brevifolia* J. Presl, Reliq. Haenk. 1 (4–5): 248. 1830.

Cinnagrostis brevifolia var. **expansa** (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia brevifolia* var. *expansa* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 125. 1995.

Cinnagrostis cabrerae (Parodi) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis cabrerae* Parodi, Revista Argent. Agron. 15 (1): 59, f. 3. 1948.

Cinnagrostis cabrerae var. **aristulata** (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia cabrerae* var. *aristulata* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 126, f. 1. 1995.

Cinnagrostis cabrerae var. **maxima** (Rúgolo) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia cabrerae* var. *maxima* Rúgolo, Parodiana 4 (1): 106, f. 3a–e. 1986.

Cinnagrostis cabrerae var. **trichopoda** (Parodi ex Rúgolo) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia cabrerae* var. *trichopoda* Parodi ex Rúgolo, Parodiana 4 (1): 107, f. 3f–k. 1986.

Cinnagrostis calderillensis (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis calderillensis* Pilg., Bot. Jahrb. Syst. 42 (1): 72. 1908.

Cinnagrostis chrysophylla (Phil.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia chrysophylla* Phil., Verz. Antofagasta Pfl. 83. 1891.

Cinnagrostis ciliata (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia ciliata* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 126, f. 2. 1995 (≡ *Calamagrostis cordechii* Govaerts).

Cinnagrostis ciliata var. **glabrescens** (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia ciliata* var. *glabrescens* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 128, f. 3. 1995.

Cinnagrostis coarctata (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia coarctata* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 143. 1815 (1816) (≡ *Calamagrostis fibrovaginata* Lægaard, non *Calamagrostis coarctata* Eaton).

Cinnagrostis crispa (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia crispa* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 128, f. 4. 1995.

Cinnagrostis cryptolopha (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis cryptolopha* Wedd., Bull. Soc. Bot. France 22: 176, err. typ. 156, 179. 1875.

Cinnagrostis curta (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia curta* Wedd., Bull. Soc. Bot. France 22: 156 (176), 179. 1875.

Cinnagrostis curvula (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia curvula* Wedd., Bull. Soc. Bot. France 22: 178, 179. 1875.

Cinnagrostis cuzcoensis (Tovar) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis cuzcoensis* Tovar, Publ. Mus. Hist. Nat. Javier Prado, Ser. B, Bot. 33: 11. 1985.

Cinnagrostis densiflora (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia densiflora* J. Presl, Reliq. Haenk. 1 (4–5): 247. 1830.

Cinnagrostis deserticola (Phil.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia deserticola* Phil., Fl. Atacam. 55. 1860.

Cinnagrostis deserticola var. **breviaristata** (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia deserticola* var. *breviaristata* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 134, f. 6. 1995.

Cinnagrostis divergens (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis divergens* Swallen, Contr. U.S. Natl. Herb. 29 (6): 262–263. 1948 (1949).

Cinnagrostis fiebrigii (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis fiebrigii* Pilg., Bot. Jahrb. Syst. 42 (1): 68. 1908.

Cinnagrostis filifolia (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia filifolia* Wedd., Bull. Soc. Bot. France 22: 178, 179. 1875 [= *Calamagrostis amoena* (Pilg.) Pilg.].

Cinnagrostis filifolia var. **festucoides** (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia festucoides* Wedd., Bull. Soc. Bot. France 22: 178, 179. 1875 [= *Calamagrostis amoena* var. *festucoides* (Wedd.) Soreng].

Cinnagrostis fuscata (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia fuscata* J. Presl, Reliq. Haenk. 1 (4–5): 249. 1830.

Cinnagrostis glacialis (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia glacialis* Wedd., Bull. Soc. Bot. France 22: 178–179. 1875.

Cinnagrostis heterophylla (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia heterophylla* Wedd., Bull. Soc. Bot. France 22: 177, 180. 1875 (= *Calamagrostis swallenii* Tovar).

Cinnagrostis hieronymi (Hack.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis hieronymi* Hack., Oesterr. Bot. Z. 52 (3): 109. 1902.

Cinnagrostis hirsuta (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia hirsuta* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 136, f. 7. 1995 (≡ *Calamagrostis menhoferi* Govaerts).

Cinnagrostis hirta (Sodiro) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia hirta* Sodiro, Revista Colegio Nac. Vicente Rocafuerte 12: 64, 75. 1930.

Cinnagrostis intermedia (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia intermedia* J. Presl, Reliq. Haenk. 1 (4–5): 249. 1830.

Cinnagrostis involuta (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis involuta* Swallen, Contr. U.S. Natl. Herb. 29 (6): 259. 1948 (1949).

Cinnagrostis jamesonii (Steud.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis jamesonii* Steud., Syn. Pl. Glumac. 1: 191. 1855 (1854).

Cinnagrostis lagurus (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia lagurus* Wedd., Bull. Soc. Bot. France 22: 156 (176). 1875 (≡ *Calamagrostis cephalantha* Pilg.).

Cinnagrostis leiophylla (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia leiophylla* Wedd., Bull. Soc. Bot. France 22: 177, 180. 1875.

Cinnagrostis macrophylla (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia macrophylla* Pilg., Bot. Jahrb. Syst. 25 (5): 711–712. 1898.

Cinnagrostis macrostachya (Sodiro) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia macrostachyum* Sodiro, Revista Colegio Nac. Vicente Rocafuerte 12: 64, 74. 1930.

Cinnagrostis malamalensis (Hack.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis malamalensis* Hack., Anales Mus. Nac. Buenos Aires 13: 478. 1906.

Cinnagrostis mandoniana (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia mandoniana* Wedd., Bull. Soc. Bot. France 22: 179, 180. 1875.

Cinnagrostis micrathera (E. Desv.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum micratherum* E. Desv., Fl. Chil. 6: 352. 1854 (≡ *Leptophyllochloa micrathera* (E. Desv.) C.E. Calderón).

Cinnagrostis minima (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis vicunarum* var. *minima* Pilg., Pilg. Bot. Jahrb. Syst. 42: 63. 1908.

Cinnagrostis mollis (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis mollis* Pilg., Bot. Jahrb. Syst. 42 (1): 61. 1908.

Cinnagrostis mulleri (Luces) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis mulleri* Luces, Bol. Soc. Venez. Ci. Nat. 15 (80): 9–11, f. 5. 1953.

Cinnagrostis nitidula (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis nitidula* Pilg., Bot. Jahrb. Syst. 42 (1): 69. 1908.

Cinnagrostis orbignyana (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia orbignyana* Wedd., Bull. Soc. Bot. France 22: 178, 180. 1875.

Cinnagrostis patagonica (Speg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Deyeuxia patagonica* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 7: 191. 1902.

Cinnagrostis polygama (Griseb.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Cinnagrostis polygama* Griseb., Abh. Königl. Ges.Wiss. Göttingen 19: 257, t.2, f. 7. 1874. **Figure 1A–G**.

Cinnagrostis polygama var. **filifolia** (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia polygama* var. *filifolia* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31(1–2): 139, f. 8. 1995.

Cinnagrostis preslii (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Agrostis preslii* Kunth, Enum. Pl. 1: 225. 1833 (≡ *Agrostis caespitosa* J. Presl, nom. illeg. hom. non. (L.) Salisb. ≡ *Deyeuxia nana* Rúgolo).

Cinnagrostis rauhii (Tovar) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis rauhii* Tovar, Mem. Mus. Hist. Nat. "Javier Prado" 11: 78. 1960.

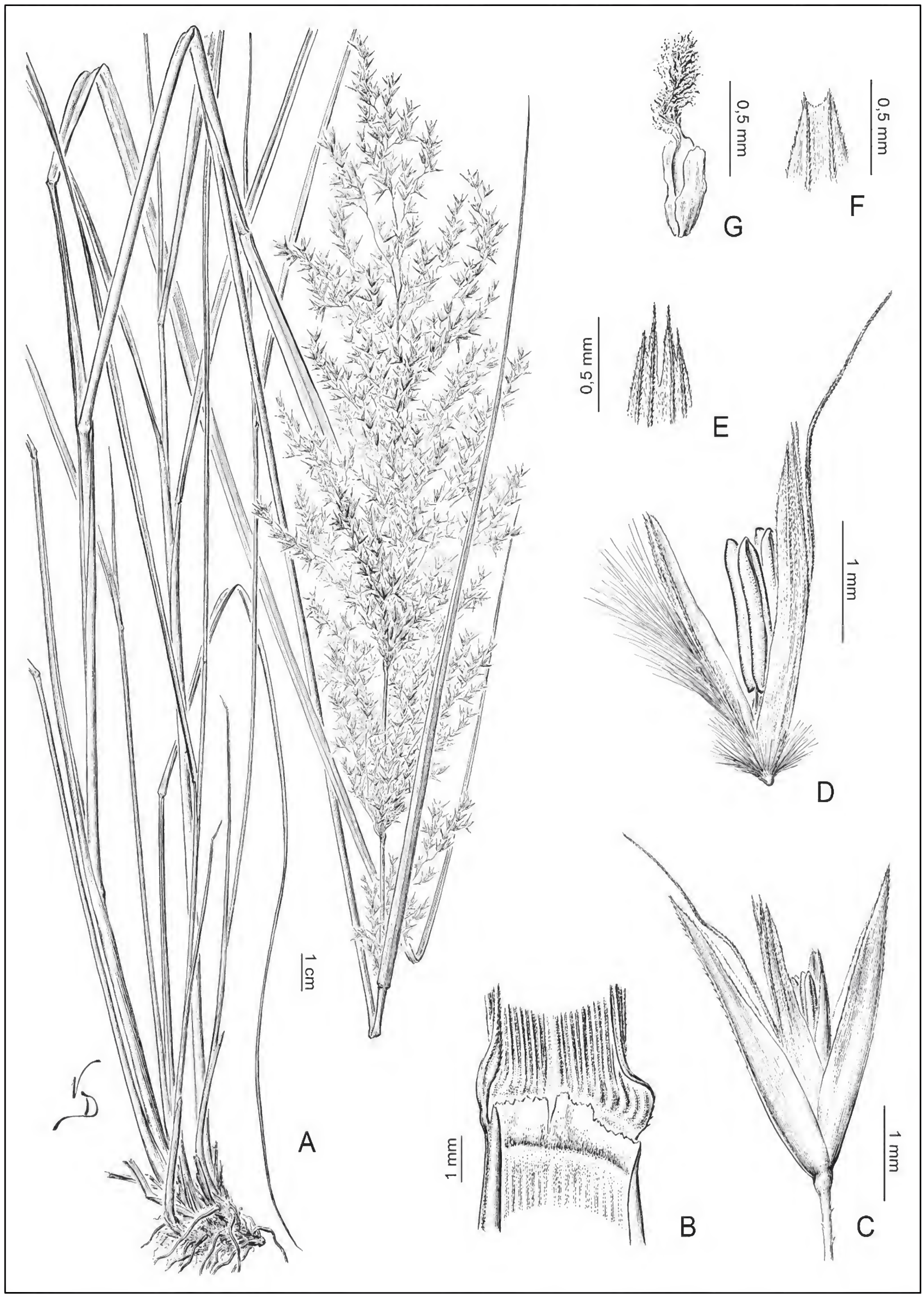

Figure 1. Illustration of *Cinnagrostis polygama* from Argentina; drawn by Victor Dudas. A. Habit. B. Ligule. C. Spikelet. D. Floret. E. Lemma apex. F. Palea apex. G. Pistil and lodicules.

Cinnagrostis recta (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia recta* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 144–145. 1815 (1816).

Cinnagrostis reitzii (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis reitzii* Swallen, Sellowia 7: 11. 1956.

Cinnagrostis rigescens (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Agrostis rigescens* J. Presl, Reliq. Haenk. 1 (4–5): 237. 1830.

Cinnagrostis rigida (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia rigida* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 144. 1815 (1816).

Cinnagrostis rosea (Griseb.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Agrostis rosea* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 253–254. 1874.

Cinnagrostis rupestris (Trin.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis rupestris* Trin., Gram. Panic. 28. 1826.

Cinnagrostis scaberula (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis scaberula* Swallen, Contr. U.S. Natl. Herb. 29 (6): 261. 1948 (1949).

Cinnagrostis sclerantha (Hack.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis sclerantha* Hack., Oesterr. Bot. Z. 52 (3): 108. 1902.

Cinnagrostis setiflora (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia setiflora* Wedd., Bull. Soc. Bot. France 22: 176, 180. 1875.

Cinnagrostis spicigera (J. Presl) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia spicigera* J. Presl, Reliq. Haenk. 1 (4–5): 247. 1830.

Cinnagrostis spicigera var. **cephalotes** (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia cephalotes* Wedd., Bull. Soc. Bot. France 22: 178, 179. 1875.

Cinnagrostis steyermarkii (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Calamagrostis steyermarkii* Swallen, Contr. U.S. Natl. Herb. 29 (6): 258–259. 1948 (1949).

Cinnagrostis tarmensis (Pilg.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis tarmensis* Pilg., Bot. Jahrb. Syst. 42 (1): 70. 1908.

Cinnagrostis tarmensis var. **macrochaeta** (Hack. ex R.E. Fr.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis rosea* var. *macrochaeta* Hack. ex R.E. Fr., Ark. Bot. 8 (8): 40. 1908 (1909).

Cinnagrostis trichodonta (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia trichodonta* Wedd., Bull. Soc. Bot. France 22: 156 (176), 180. 1875.

Cinnagrostis trichodonta var. **hirsuta (**Rúgolo) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia trichodonta* var. *hirsuta* Rúgolo, Darwiniana 44(1): 254, f. 47. 2006.

Cinnagrostis velutina (Nees & Meyen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia velutina* Nees & Meyen, Gramineae 15–16. 1841.

Cinnagrostis velutina var. **nardifolia** (Griseb.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Agrostis nardifolia* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 252–253. 1874.

Cinnagrostis vicunarum (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia vicunarum* Wedd., Bull. Soc. Bot. France 22: 177, 180. 1875.

Cinnagrostis violacea (Wedd.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia violacea* Wedd., Bull. Soc. Bot. France 22: 179, 180. 1875.

Cinnagrostis violacea var. **puberula** (Rúgolo & Villav.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia violacea* var. *puberula* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31 (1–2): 139. 1995.

Cinnagrostis viridiflavescens (Poir.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Arundo viridiflavescens* Poir., Encycl. 6: 271. 1804.

Cinnagrostis viridiflavescens var. **montevidensis** (Nees) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis montevidensis* Nees, Fl. Bras. Enum. Pl. 2 (1): 401. 1829.

Cinnagrostis viridis (Phil.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia viridis* Phil., Linnaea 33 (3–4): 288. 1865.

DESCHAMPSIA P.Beauv., Ess. Agrostogr. 91, pl. 18, f. 3. 1812. TYPE: *Deschampsia cespitosa* (L.) P. Beauv. [≡ *Aira cespitosa* L. ≡ *Agrostis caespitosa* (L.) Salisb. ≡ *Avena caespitosa* (L.) Kuntze ≡ *Campella caespitosa* (L.) Link ≡ *Podionapus caespitosus* (L.) Dulac].

Comments—We report 12 western hemisphere taxa usually treated in *Calamagrostis, Deyeuxia,* or *Scribneria* Hack., transferred into *Deschampsia* by Saarela et al. (2017), along with new combinations, all except three supported by our molecular phylogeny (Romaschenko et al. in prep). Two morphologically similar taxa published by Sylvester (2019) have not yet been tested. We choose not to emend the generic description at this time but note all these species of *Deschampsia* (subtribe. Aristaveninae F. Albers & Butzin) generally have 1(−2)-flowered spikelets, stipitate basal florets [the rachilla below the floret is slightly elongated raising it above the glumes as in *Stylagrostis* Mez], long membranous ligules (usually 6−20 mm long), smooth or nearly so, glabrous, often with flanking auriculate lobes and decurrent along the sheath margins, shinny and lustrous glumes (Escalona 1988; Saarela et al. 2017), and caryopses with solid endosperm.

Deschampsia ampliflora (Tovar) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.*** Basionym: *Calamagrostis amplifora* Tovar, Mem. Mus. Hist. Nat. Javier Prado 11: 16. 1960.

Deschampsia aurea (Munro ex Wedd.) Saarela, PhytoKeys 87: 87. 2017. Basionym: *Deyeuxia aurea* Munro ex Wedd., Bull. Soc. Bot. France 22: 176 (156), 179. 1875 (1876).

Deschampsia bolanderi (Thurb.) Saarela, PhytoKeys 87: 90. 2017. Basionym: *Lepturus bolanderi* Thurb., Proc. Amer. Acad. Arts 7: 401. 1868. [≡ *Scribneria bolanderi* (Thurb.) Hack.].

Deschampsia boyacensis (Swallen & García-Barr) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.*** Basionym: *Calamagrostis boyacensis* Swallen & García-Barr, Caldasia 2(8): 302, f. D. 1943.

Deschampsia chrysantha (J. Presl) Saarela, PhytoKeys 87: 88. 2017. Basionym: *Deyeuxia chrysantha* J. Presl, Reliq. Haenk. 1 (4−5): 247. 1840.

Deschampsia chrysantha var. *phalaroides* (Wedd.) Saarela, PhytoKeys 87: 88. 2017. Basionym: Wedd. Bull. Soc. Bot. France 22: 177, 180. 1875.

Deschampsia chrysostachya (E. Desv.) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.** Basionym: *Deyeuxia chrysostachya* E. Desv. Fl. Chil. 6: 323, t. 78, f. 2. 1854.

Deschampsia eminens (J. Presl) Saarela, PhytoKeys 87: 89. 2017. Basionym: *Deyeuxia eminens* J. Presl, Reliq. Haenk. 1 (4–5): 250. 1830.

Deschampsia eminens var. **discreta** (Rúgolo & Villav.) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.** Basionym: *Deyeuxia eminens* var. *discreta* Rúgolo & Villav., Bol. Soc. Argent. Bot. 31(1–2): 135. 1995.

Deschampsia eminens var. *fulva* (Griseb.) Saarela, PhytoKeys 87: 89. 2017. Basionym: *Agrostis fulva* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 294. 1879.

Deschampsia eminens var. *inclusa* (Rúgolo) Saarela, PhytoKeys 87: 90. 2017. Basionym: *Deyeuxia eminens* var. *inclusa* Rúgolo, Darwiniana 44 (1): 195, f. 24. 2006.

Deschampsia gayana (Steud.) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.** Basionym: *Aira gayana* Steud., Syn. Pl. Glumac. 1: 220. 1855 (1854). (other name: *Deyeuxia erythrostachya* E. Desv.).

Deschampsia gayana var. **neuquenensis** (Rúgolo) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.*** Basionym: *Deyeuxia erythrostachya* var. *neuquenensis* Rúgolo, Darwiniana 19(2–4): 410, f. 3. 1975.

Deschampsia hackelii (Lillo) Saarela, Phytokeys 87: 87. 2017. Basionym: *Calamagrostis hackelii* Lillo, Anales Mus. Nac. Buenos Aires 21: 100, t. 4, f. A. 1–5. 1911.

Deschampsia ovata (J. Presl) Saarela, PhytoKeys 87: 88. 2017. Basionym: *Deyeuxia ovata* J. Presl, Reliq. Haenk. 1(4–5): 246. 1830.

Deschampsia ovata var. *nivalis* (Wedd.) Saarela, PhytoKeys 87: 88. 2017. Basionym*: Deyeuxia nivalis* Wedd., Bull. Soc. Bot. France 22: 176, 180. 1875.

Deschampsia parodiana (Kunth) Saarela, PhytoKeys 87: 90. 2017. Basionym: *Deyeuxia ligulata* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 145. 1815 (1816).

Deschampsia podophora (Pilg.) Saarela, PhytoKeys 87: 90. 2017. Basionym: *Calamagrostis podophora* Pilg., Bot. Jahrb. Syst. 42 (1): 66. 1908.

Deschampsia podophora var. *mutica* Sylvester*, PhytoKeys 122: 63−66, f. 3. 2019.

Deschampsia santamartensis Sylvester & Soreng*, PhytoKeys 122: 56−59, f. 2. 2019.

Deschampsia teretifolia (Lægaard) Romasch., P.M. Peterson, Soreng & Barberá, **comb. nov.** Basionym: *Calamagrostis teretifolia* Lægaard, Novon 8 (1): 27, f. 1E. 1998.

GREENEOCHLOA P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov.** **TYPE**: *Greeneochloa coarctata* (Eaton) P.M. Peterson, Soreng, Romasch. & Barberá (≡ *Calamagrostis coarctata* Eaton).

Diagnosis—Differing from *Calamagrostis* Adans. in having hairy ovaries, extravaginal shoot innovations, flat leaf blades, and panicles contracted usually with ascending tightly appressed or slightly spreading branches.

Description—Loosely cespitose perennials with rhizomes 1−10 cm long, 2−4 mm thick. Culms (47−)60−200 cm tall, 3−8 mm in diameter, unbranched, smooth to scabrous with extravaginal shoot innovations below; nodes 2−5(−6), glabrous. Leaf sheaths shorter than the internodes, smooth or scabrous, sometimes inflated near summit, glabrous or sparingly hairy, culm sheath margins fused at the base for a few mm; collars smooth to scabrous, sometimes hairy; ligules (1−)3−6(−12) mm long, hyaline to chartaceous, obtuse to truncate, rarely acute, often erose or lacerate, abaxially scabrous to scaberulous; blades (3−)4−35(−45) cm long, (2−)3−15 mm wide, flat, glabrous below, glabrous and scabrous to hairy above, margins sometimes hairy. Panicles 7−25 cm long, (0.8−)1−3 cm wide, terminal, contracted sometimes interrupted near base, greenish to purplish or yellowish; branches ascending and loosely to tightly appressed, nearly smooth to densely scabrous, sometimes naked below. Spikelets (4.5−)5−8(−9) mm long, 1(−2)-flowered, laterally compressed; rachilla prolongation (0.5−)1−2(−4) mm long, hairy or glabrous and hairy at the apex, the hairs 1−4 mm long, whitish; disarticulation above the glumes; glumes usually longer to as long as the florets, acuminate, scabrous along the midvein, margins often hyaline; lower glumes 1 or 3-veined; upper glumes usually 3-veined; lemmas 4−6.5(−7.5) mm long, lanceolate, chartaceous to membranous, scaberulous, 5-veined, dorsally awned from the lower 1/5 to upper ¾ or at the apex, the awns 1−10 mm long, straight or bent, apex entire or 4-toothed; callus hairy, the hairs (0.8−)1−5 mm long; paleas shorter than the lemmas, 2-keeled, apex acuminate, body sub-chartaceous or scareous, gap between keels about as broad as outer flanges; stamens 3, anthers 1.5−4 mm long; ovaries with scattered or dense hairs, at least at the apex, styles 2, stigmas feathery; lodicules 2, membranous, lobed, glabrous or pubescent. Caryopses 2−3 mm long, ovoid to fusiform, slightly compressed, sulcus prominent, hilum 1/3 the grain in length, endosperm dry, hard, pericarp adherent.

Etymology—The new genus honors Craig William Greene (1949−2003), an American taxonomist who focused on agamic complexes in polyploid species of *Calamagrostis* and *Amelanchier* Medik.

Distribution—*Greeneochloa* occurs in Oregon, Washington, and Montana (*G. tweedyi*), and extending in eastern North America from Nova Scotia and Maine to Georgia and Louisiana (*G. coarctata*) [Marr. et al. 2007].

Comments—In Romaschenko et al. (in prep.) the two species of *Greeneochloa* form a clade within subtribe Echinopogoninae which is sister to subtribe Calothecinae plus *Calamagrostis* s.s. (subtribe. Agrostidinae Fr.) all in supersubtrib. Agrostidodinae Soreng [Soreng et al. 2017; Peterson al. in prep.].

Greeneochloa coarctata (Eaton) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis coarctata* Eaton, Man. Bot. 144. 1829 (*Calamagrostis cinnoides* W.P.C. Barton is misapplied to this species ≡ *Calamagrostis canadensis* Michx.). Figure 2.

Figure 2. *Greeneochloa coarctata* collected *by L.J. Lehtonen & S.M. Young 62* (US) in Maryland, USA.

Greeneochloa tweedyi (Scribn.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia tweedyi* Scribn., Bull. Torrey Bot. Club 10: 64. 1883 [≡ *Calamagrostis tweedyi* (Scribn.) Scribn.].

LAEGAARDIA P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov. TYPE**: *Laegaardia ecuadoriense* (Lægaard) P.M. Peterson, Soreng, Romasch. & Barberá (≡ *Calamagrostis ecuadoriensis* Lægaard).

Diagnosis—Differing from *Paramochloa* P.M. Peterson, Soreng, Romasch. & Barberá in having unawned lemmas, two 3-veined glumes, and culms 11−42 cm tall.

Description—Cespitose perennials. Culms 11−42 cm tall, about 1 mm diameter, erect, furrowed, smooth to hispid with intravaginal shoot innovations below. Basal leaves with short sheaths, the sheaths 2−3(−5) cm long, shallowly furrowed, glabrous, fibrous in age; ligules 0.5−1 mm long, truncate; collar distinct ±swollen; leaf blades 3−7 cm long, 0.3−1 mm wide, tightly involute, abaxially furrowed, glabrous, adaxially deeply furrowed, finely hispid. Culm leaves with long sheaths, upward slightly inflated, membranous; auricles higher than ligule; leaf blades 1−5 cm long, involute; flag leaf 1–1.5 cm long. Panicles 8−14 cm long, 0.7−1.6 cm wide, narrow, the axis, branches and pedicels glabrous to hispid, usually dark purplish; branching verticillate on lower nodes. Spikelets 1(2)-flowered, laterally compressed; rachilla prolongation 1.4−1.6 mm long with hairs almost reaching the apex of the lemma; disarticulation above the glumes; glumes 3.5−4 mm,long, subequal, both 3-veined with lateral veins rather faint, broadly lanceolate, apex obtuse to acute, finely erose, keeled toward apex, scabrid and mat on and between veins, glabrous and shining along margin; floret on short stipe about 0.15 mm long; lemmas 2.7−3.1 mm long, ovate, membranous, 5-veined, apex obtuse,to irregularly minutely-toothed, scabrid on back, awn lacking; callus hairy, the hairs 1−1.5 mm long; paleas 1.9–2.7 mm long, shorter than the lemma, 2-veined, scareous, keels scabrid with a narrow gap between them and broad lateral flanges; stamens 3, anthers 0.8−1 mm long, purple; ovaries glabrous, styles 2, distinctly gapped, stigmas feathery; lodicules 2, membranous. Caryopses 1.2−1.4 mm long, elliptical-ovoid, slightly compressed, sulcate, hilum linear 1/3 the grain in length, embryo small, endoperm solid, pericarp adherent.

Etymology—The new genus honors Simon Lægaard (1933–), a renowned Danish Botanist, who has made extensive collections in Ecuador, Greenland, and South America.

Distribution—The single species in *Laegaardia* is endemic to Ecuador where it has been found in the Provinces of Azuay, Chimborazo, Loja [*Lægaard 18999, 19111, 19339* (AAU, QCA, US)], Napo, and Pichincha (Lægaard 1998).

Comments—*Laegaardia ecuadoriense* is a strongly supported sister to *Paramochloa crispifolia* (Sylvester) P.M. Peterson, Soreng, Romasch. & Barberá plus *P. effusa* (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá within subtribe Calothecinae (Soreng 2015; Romaschenko et al. in prep.).

Laegaardia ecuadoriense (Lægaard) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis ecuadoriensis* Lægaard, Novon 8 (1): 25–26, f. 1B. 1998. **Figure 3**.

PARAMOCHLOA P.M. Peterson, Soreng, Romasch. & Barberá, **gen. nov. TYPE**: *Paramochloa effusa* (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá [≡ *Deyeuxia effusa* Kunth ≡ *Calamagrostis effusa* (Kunth) Steud.].

Diagnosis—Differing from *Laegaardia* P.M. Peterson, Soreng, Romasch. & Barberá in having awned lemmas, 1-veined lower glumes, and culms 40−100 cm tall.

Figure 3. Isotype of *Laegaardia ecuadoriense* collected by *S. Lægaard 53295* (US) in Ecuador.

Description—Cespitose perennials, forming dense mats sometimes appearing below as short vertical or oblique rhizomes. Culms 40−100 cm tall, 1−2.5 mm diameter, erect, smooth, with intravaginal shoot innovations below. Basal leaf sheaths becoming fibrous below, the sheaths shorter than the internodes; ligules 2.2−10 mm long, truncate, obtuse to acute; leaf blades 5−30 cm long, 0.5−3 mm wide, involute, stiffly erect or strongly curled, readily or tardily deciduous with age breaking off at ligule insertion tending to form a J at base after falling leaving the ligule exposed. Panicles (5.5−)9−20 cm long, 3−10 cm wide, open to somewhat contracted, the axis, branches and pedicels terete, smooth to scabrous, purplish; branching verticillate on lower nodes. Spikelets 1-flowered, not strongly laterally compressed; rachilla prolongation 1.6−5.5 mm long, hairy, the hairs 0.5−1.2 mm long, sometimes exceeding the apex of the lemma; disarticulation above the glumes; glumes 3−5.5 mm long, as long or longer than the florets, subequal, lanceolate, membranous, scaberulous distally, purplish, lustrous; lower glumes 1-veined; upper glumes 3-veined, the lateral veins present on lower 1/3−1/2, with 1 or 2 cross veins between the keel and lateral vein infrequently present in ca. 10% of spikelets seen (requires 25x magnification); floret sessile; lemmas 2.9−4.6 mm long, 5-veined, lanceolate, membranous, glabrous to scabrous, lustrous, awned dorsally, apex emarginate with finely denticulate lobes; awns 2−7.2 mm long, inserted from near the middle, geniculate and twisted near base; callus rounded with a tuft of hairs, the hairs 0.2−0.8 mm long; paleas shorter than the lemma, 2-veined, membranous, apex bidentate; stamens 3, anthers 1.5−2.7 mm long; ovaries glabrous, styles 2, separated, stigmas feathery; lodicules 2, 2-lobed, membranous. Caryopses 1.8−2 mm long, ovate, sulcus shallow, hilum linear, 1/3-1/2 the grain in length, embryo small, endosperm dry, hard, pericarp adherent.

Distribution—The two South American species of *Paramochloa* occur in the paramos of Colombia, Ecuador, and Venezuela.

Comments—In a molecular phylogeny based on four gene regions (ITS, *rpl32-trnL* spacer, *rps16-trnK* spacer, and *rps16* intron), *Paramochloa crispifolia* and *P. effusa* form a clade sister to *Laegaardia ecuadoriense* within subtribe Calothecinae (Romaschenko et al. in prep.).

Paramochloa crispifolia (Sylvester) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis crispifolius* Sylvester, PhytoKeys 122: 51−54, f. 1. 2019.

Paramochloa effusa (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia* effusa Kunth, Nov. Gen. Sp. (quarto ed.) 1: 146, t. 46. 1815 (1816). **Figure 4**.

PEYRITSCHIA E. Fourn., Mexic. Pl. 2: 109. 1886, **gen. emend.** **TYPE**: *Peyritschia koelerioides* (Peyr.) E. Fourn. (≡ *Aira koelerioides* Peyr.).

Description—Perennials, cespitose or with short rhizomes. Culms 5−300 cm tall, glabrous or pubescent. Leaf blades flat, conduplicate, convolute or involute, soft, rarely rigid; ligule membranous. Panicles narrow, contracted to open and ovate to pyramidal. Spikelets 3−10 mm long, 1−6-flowered, laterally compressed; rachilla hairy, rarely glabrous to scabrous, usually prolonged above the upper floret (usually to ¾ the length of the lemma in single-flowered species); disarticulation above the glumes and between the florets; glumes usually longer than the lower floret, isomorphic or dimorphic, the lower 1 or 3-veined, the upper 1, 3 or 5-veined; basal floret often short stipitate; lemmas (3)5(7)-veined, usually awned from the back, the central awn often geniculate or divaricate, apex entire or sometimes with 2−4 short awns (extension of the lateral veins); callus usually short pilose or pubescent, sometimes glabrous; paleas usually shorter than the lemma, tightly enclosed by margins of the lemma or loosely enclosed, 2-keeled, hyaline; stamens 2 or 3, anthers 0.5−3.5 mm long; lodicules 2, membranous; ovary glabrous or hairy. Caryopses compressed, hilum < 1/5 the grain in length, endosperm liquid, soft or pasty, or hard, pericarp adherent. Basic chromosome number $x = 7$.

Figure 4. *Paramochloa effusa* collected by *J. Cuatrecasas 18982* (USF) in Dpto. Cauca, Colombia.

Distribution—Species of *Peyritschia* primarily range throughout Mexico and Central America with a few species extending into South America as far south as Bolivia.

Comments—In Romaschenko et al. (in prep.) the former Mexican and Central American species of *Trisetum*, *Calamagrostis*, and those previously placed in *Peyritschia* form a clade (*Peyritschia* clade) sister to *Cinnagrostis* within the Koeleriinae clade B of the Aveninae (Finot et al. 2004, 2006; Peterson et al. 2004; Romaschenko et al. in prep.). The traditional seven species treated in *Peyritschia* s.s. (Finot et al. 2004, 2006) also form a clade nested within the expanded *Peyritschia* s.l. treated here.

Peyritschia angusta (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Trisetum angustum* Swallen, Phytologia 4 (7): 423. 1953.

Peyritschia bealii P.M. Peterson, Soreng, Romasch. & Barberá, **nom. nov.** Basionym: *Calamagrostis pringlei* Scribn. ex Beal, Grass. N. Amer. 2: 345. 1896.

Peyritschia coahuilensis (P.M. Peterson, Soreng, & Valdés-Reyna) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis coahuilensis* P.M. Peterson, Soreng, & Valdés-Reyna, Sida 21 (1): 312, 314, f.1. 2004.

Peyritschia conferta (Pilg.) Finot, Contr. U.S. Natl. Herb. 48: 478. 2003. Basionym: *Trisetum confertum* Pilg., Bot. Jahrb. Syst. 25 (5): 714. 1898.

Peyritschia curviseta (Morden & Valdés-Reyna) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum curvisetum* Morden & Valdés-Reyna, Brittonia 35 (4): 375, f.1. 1983.

Peyritschia deyeuxioides (Kunth) Finot, Contr. U.S. Natl. Herb 48: 478. 2003. Basionym: *Avena deyeuxioides* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 147 1815 (1816) [≡ *Trisetaria deyeuxioides* (Kunth) Poir. ≡ *Trisetum deyeuxioides* (Kunth) Kunth].

Peyritchia divaricata (P.M. Peterson & Soreng) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis divaricata* P.M. Peterson & Soreng, Sida 21 (1): 315, f. 3. 2004.

Peyritschia durangensis (Finot & P.M. Peterson) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum durangense* Finot & P.M. Peterson, Ann. Missouri Bot. Gard. 91 (1): 19–21, f.2. 2004. **Figure 5A–N**.

Peyritschia erectifolia (Hitchc.) P.M. Peterson, Soreng, Romasch. & Barberá, Romasch., **comb. nov.** Basionym: *Calamagrostis erectifolia* Hitchc., N. Amer. Fl. 17 (7): 507. 1937.

Peyritschia eriantha (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia eriantha* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 145. 1815 (1816) [≡ *Arundo eriantha* (Kunth) Poir. ≡ *Calamagrostis eriantha* (Kunth) Steud.].

Peyritschia filifolia (Scribn. ex Beal) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum filifolium* Scribn. ex Beal, Grass. N. Amer. 2: 375. 1896.

Peyritschia foliosa (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum foliosum* Swallen, Contr. U.S. Natl. Herb. 29 (6): 256–257. 1948 (1949).

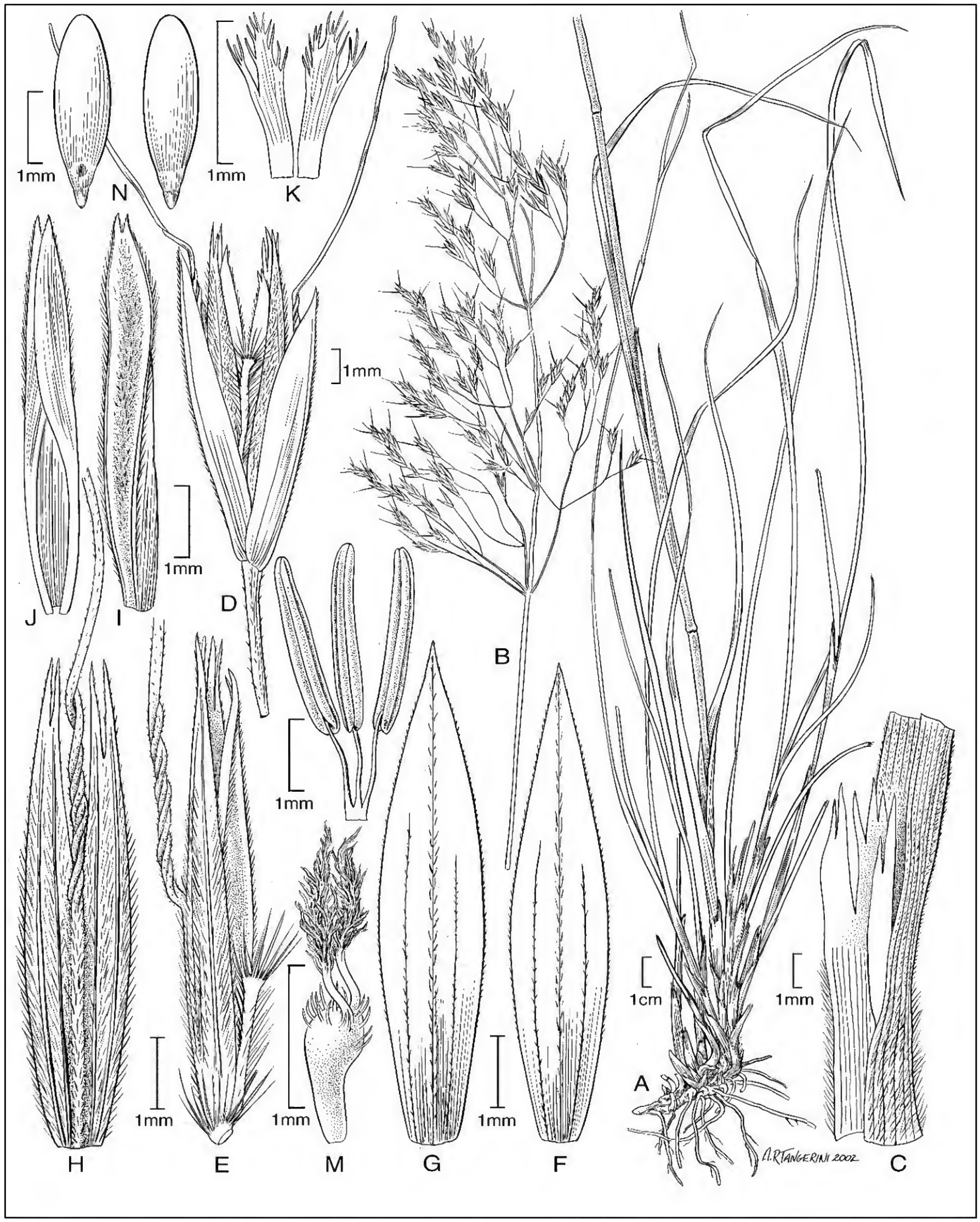

Figure 5. Holotype illustration of *Peyritschia durangensis* collected by *P.M. Peterson and C.R. Annable 6034* (US) in Durango, Mexico; drawn by Alice Tangerini. A. Habit. B. Inflorescence. C. Ligule. D. Spikelet. E. Floret. F. Lower glume. G. Upper glume. H. Lemma. I. Palea, dorsal view. J. Palea, ventral view. K. Lodicules. L. Stamens. M. Pistil. N. Caryopses.

Peyritschia graphephoroides P.M. Peterson, Soreng, Romasch. & Barberá, **nom. nov.** Basionym: *Graphephorum pringlei* Scribn. ex Beal, Grass. N. Amer. 2: 561. 1896 [≡ *Trisetum pringlei* (Scribn. ex Beal) Hitchc.], non *Peyritschia pringlei* (Scribn.) S.D. Koch.

Peyritschia howellii (Hitchc.) Finot & P.M. Peterson, Sida 22 (2) 897. 2006. Basionym: *Trisetum howellii* Hitchc., Proc. Calif. Acad. Sci., ser. 4, 21 (24): 296. 1935.

Peyritschia humilis (Louis-Marie) Finot, Contr. U.S. Natl. Herb. 48: 478. 2003. Basionym: *Trisetum humile* Louis-Marie, Rhodora 30: 244. 1928 (1929).

Peyritschia irazuense (Kuntze) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis irazuense* Kuntze, Revis. Gen. Pl. 2: 763. 1891.

Peyritschia killipii (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis killipii* Swallen, Contr. U.S. Natl. Herb. 29 (6): 257. 1948 (1949).

Peyritschia koelerioides (Peyr.) E. Fourn., Mexic. Pl. 2: 110. 1886. Basionym: *Aira koelerioides* Peyr., Linnaea 30 (1): 5–6. 1859 [≡ *Deschampsia koelerioides* (Peyr.) Benth. nom illeg. hom.] [= *Graphephorum altijugum* E. Fourn. ≡ *Trisetum altijugum* (E. Fourn.) Scribn.].

Peyritschia martha-gonzaleziae (P.M. Peterson & Finot) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.*** Basionym: *Trisetum martha-gonzaleziae* P.M. Peterson & Finot, Ann. Missouri Bot. Gard. 91 (1): 21, f.3. 2004.

Peyritschia orizabae (Rupr. ex E. Fourn.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Deyeuxia orizabae* Rupr. ex E. Fourn., Bull. Soc. Bot. France 24: 181. 1877.

Peyritschia palmeri (Hitchc.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum palmeri* Hitchc., Contr. U.S. Natl. Herb. 17(3): 325. 1913.

Peyritschia pinetorum (Swallen) Finot & P.M. Peterson, Sida 22 (2): 899. 2006. Basionym: *Trisetum pinetorum* Scribn., Phytologia 4: 424. 1953.

Peyritschia planifolia (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis planifolia* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 145 1815. (1816).

Peyritschia pringlei (Scribn.) S.D. Koch, Taxon 28 (1–3): 233. 1979. Basionym: *Deschampsia pringlei* Scribn., Proc. Acad. Nat. Sci. Philadelphia 43 (2): 300–301, t. 13, f.1, 1a. 1891 (≡ *Trisetum kochianum* Hern. Torres).

Peyritschia spellenbergii (Soreng, Finot, & P.M. Peterson) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum spellenbergii* Soreng, Finot & P.M. Peterson, Ann. Missouri Bot. Gard. 91 (1): 23–25, f.4. 2004.

Peyritschia tolucensis (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, comb. nov. Basionym: *Deyeuxia tolucensis* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 143. 1815 (1816) [≡ *Arundo tolucensis* (Kunth) Poir. ≡ *Calamagrostis tolucensis* (Kunth) Trin. ex Steud.].

Peyritschia tonduzii (Hitchc.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum tonduzii* Hitchc., N. Amer. Fl. 17 (8): 558. 1939.

Peyritschia valida (Sohns) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis valida* Sohns, J. Wash. Acad. Sci. 46 (12): 385, f. 47–55. 1956.

Peyritschia viridis (Kunth) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Avena viridis* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 147. 1815 (1816) [≡ *Trisetum viride* (Kunth) Kunth].

Peyritschia virletii (E. Fourn.) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Trisetum virletii* E. Fourn., Mexic. Pl. 2: 108. 1886.

Peyritschia vulcanica (Swallen) P.M. Peterson, Soreng, Romasch. & Barberá, **comb. nov.** Basionym: *Calamagrostis vulcanica* Swallen, Phytologia 4 (7): 424. 1953.

Unplaced taxa
Calamagrostis brevipaleata Swallen (probable syn. of *Cinnagrostis hirta*)
Calamagrostis carchiensis Lægaard (probably *Peyritschia*)
Calamagrostis chaseae Luces (probably *Calamagrostis*)
Calamagrostis cleefii Escalona (probably *Peyritschia*)
Calamagrostis diemii (Rúgolo) Soreng (probably *Calamagrostis*)
Calamgrostis fulgida Lægaard
Calamagrostis guamanensis Escalona (probably *Deschampsia*)
Calamagrostis leonardii Chase (Molecular data indicate this is a hybrid between *Cinnagrostis* and possibly *Sphenopholis* Scribn. Further study is needed to confirm this result)
Calamagrostis macbridei Tovar
Calamagrostis pisinna Swallen (probably *Peyritschia*)
Calamagrostis pungens Tovar
Calamagrostis ramonae Escalona (probably *Deschampsia*)
Calamagrostis scabriflora Swallen (probably *Calamagrostis*)
Calamagrostis suka Speg. (probably *Calamagrostis*)
Deyeuxia curtoides Rúgolo & Villav. (probably *Cinnagrostis*)
Deyeuxia pubescens Pilg. (probably *Peyritschia*, possibly a syn. of *P. planifolia*)
Deyeuxia spruceana Wedd.

Confirmed *Calamagrostis* occurring in Latin America
Calamagrostis bogotensis (Pilg.) Pilg.
Calamagrostis epigeios (L.) Roth
Calamgrostis guatemalensis Hitchc.
Calamagrostis llanganatensis Lægaard
Calamagrostis neglecta (Ehrh.) G. Gaertn., B. Mey. & Scherb. s.l. [including *Deyeuxia pooides* (Steud.) Rúgolo, *Calamagrostis stricta* (Timm) Koeler]
Calamagrostis pinetorum Swallen

Key to genera of American grasses presently or formerly treated in *Calamagrostis* or *Deyeuxia*

1. Plants from Canada or USA; caryopses hard (2).
1. Plants from Mexico, Central America or South America; caryopses soft (liquid or semi-soft) to hard (3).

2. Ovary hairy; plants rhizomatous with extravaginal branching, not tufted; lemmas awned from upper 2/5; rachilla extension glabrous except for apical tuft of hairs (*G. coarctata*), or lemmas awned from middle, callus hairs short and all blades broad and flat (*G. tweedyi*); panicles contracted ..... **Greeneochloa**

2. Ovary glabrous; plants rhizomatous or not, with or without extravaginal branching, tufted or not; lemmas awned from near base to upper 1/3; rachilla extension hairy along the length or glabrous and rudimentary but then callus with long hairs; plants not with a combination of well-developed rhizomes, exclusively extravaginal branching, short callus hairs, broad flat blades, and contracted panicles; panicles open or contracted ..... **Calamagrostis**

3. Rachilla extension rudimentary (± 1 mm long with hairs ± 3 mm long); callus hairs mostly 1.5–2 times longer than lemma, the callus indistinct, not angled downward or recurved ..... **Calamagrostis epigeios** (introduced)

3. Rachilla extension well developed (absent in *Calamagrostis llanganatensis*, short in a few other species, but then with hairs up to 1.5 mm long); callus hairs short or long (rarely absent), as much as 1.5–2 times longer than the lemma in a few species but the callus distinct and recurved (4).

4. Anthers 2, or 3 in plants from Mexico to Guatemala; lemma body strongly 5-veined, often puberulent in part ..... **Peyritschia**

4. Anthers 1 or 3, if 3 then plants not from Mexico (*Calamagrostis guatemalensis* from Guatemala); lemma body variously veined, glabrous, sometimes scabrous (5).

5. Lemmas unawned (6).

5. Lemmas awned (8).

6. Callus and rachilla glabrous (rarely with a few short callus hairs); floret stipitate; glumes and lemmas lustrous; panicles dense, short, globose; ligules usually elongated, decurrent and acute to acuminate, entire or laterally cleft, smooth or nearly so; lodicules entire ..... **Deschampsia**

6. Callus and rachilla hairy; floret stipitate or not; glumes and lemmas mat to sub-lustrous; panicles various but not globose; ligules often less than 4 mm long, decurrent or not, often truncate to obtuse, sometimes with margins taller than the midsection, usually scabrous or pubescent; lodicules often bilobate (7).

7. Florets with a short stipe (± 0.15 mm long) between the upper glume and the callus of the floret; both glumes 3-veined; caryopsis hard, hilum linear ± 1/3 the grain in length; plants from the páramo in Ecuador ..... **Laegaardia**

7. Florets sessile; lower glumes 1-veined, upper glumes 1 or 3-veined; caryopses hard to pasty, hilum oval to punctiform < 1/4 the grain in length; plants from various locations ..... **Cinnagrostis**

8. Leaf blades readily to tardily disarticulating from collars in age (tending to form a J at base after falling), involute, sometimes sinuous; caryopsis hard, hilum linear ± 1/3 the grain in length; lower glumes 1-veined, upper glumes 3-veined and sometimes with 1 or 2 cross-veins between them; lemmas awned from middle, the awns 2–7.2 mm long, basally twisted, geniculate; callus hairs 0.2–0.8 mm long; rachillas nearly as long as lemma, densely and evenly hairy with hairs 0.5–1.2 mm long; panicles open, diffuse; plants from the páramo of Colombia, Ecuador, and Venezuela ..... **Paramochloa**

8. Leaf blades not disarticulating from collars in age, flat, folded or involute, not sinuous; caryopsis soft or hard; hilum elliptical, oval, round to punctiform 1/5–1/3 the grain in length; lower glumes 1–3-veined without cross-veins between them; lemmas awned from near base to upper 1/3, the awns 1–10 mm or more long, straight, sinuous or geniculate; callus hairs absent to 4 mm long; rachillas mostly less than ¾ the lemma in length, variously hairy, the hairs 0.5–4 mm long, sometimes reduced or absent proximally; panicles open (infrequently diffuse) or contracted; plants of various habitats, from Mexico to Tierra del Fuego, Argentina (9).

9. Florets (occasionally a second floret developed in some spikelets) with a stipe between the upper glume and the callus of the floret; glumes and lemmas lustrous, smooth or keels sparsely scaberulous; lemma awns slender, not geniculate, sometimes rudimentary or absent; blades flat or somewhat rolled inward, prominently ridged adaxially, more or less smooth (often with papillae on the long-cells between ridges); ligules slightly to strongly decurrent, usually elongated, 4–20 mm long, acuminate, smooth or nearly so, glabrous, entire or laterally cleft; lodicules, glabrous …….. **Deschampsia**
9. Florets sessile (very rarely with a second floret developed in some spikelets), rarely with a stipe to 0.2 mm long; glumes sometimes lustrous, usually scabrous at least on the keels, lemmas usually mat; blades flat to involute, smooth or scabrous, often densely so (papillae absent so far as known); ligules decurrent or not, 0.2–10 (–15) mm long, commonly less than 4 mm long (lateral lobes often exceeding the central part), often scabrous or pubescent, commonly truncate to obtuse; lodicules entire or lobed (10).

10. Caryopses hard, distinctly sulcate, hilum 1/6–1/3 the grain in length; lemmatal awns strait or slightly bent, readily distinguished from callus hairs, inserted from near base to middle, not or slightly exceeding the lemma apex; callus hairs 0.1–3 mm long 1/10–3/4 as long as the lemma in length; rachilla glabrous, or sparsely to densely hairy, hairs not reaching lemma apex; panicles contracted; anthers 1 or 3; lodicules entire and lanceolate, sometimes with an isolated lateral lobe, glabrous ..... **Calamagrostis**
10. Caryopses soft (liquid or semi-soft) or hard, sulcate (often shallowly) or not, hilum 1/6–1/4 the grain in length (often obscure in species with lipid); lemmatal awns sometimes indistinguishable from callus hairs, straight, sinuous or geniculate, capillary or stout, inserted from base to upper 1/3, usually exceeding the lemma and often exerted from the glumes; callus hairs shorter to exceeding the lemma in length; rachilla hairy, hairs often reaching 3/4 to exceeding the lemma length; panicles contracted or open; anthers 3; lodicules apically bilobate or bidentate, infrequently entire and lanceolate, apical margin sometimes ciliolate or ciliate ..... **Cinnagrostis**

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FIRST REPORT OF *CEPHALOTAXUS HARRINGTONIA* (CEPHALOTAXACAE) SPONTANEOUS IN NORTH AMERICA AND POTENTIALLY INVASIVE

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ABSTRACT

Cephalotaxus harringtonia, Japanese Plum Yew, is escaped from cultivation and naturalizing in Bronx County, New York. This study documented 65 spontaneous individuals within an area of approximately 121 hectares (300 acres). The species is documented with herbarium specimens preserved in the William and Lynda Steere herbarium at the New York Botanical Garden and photographs in the global community science program, iNaturalist. This is the first report of the species naturalized in North America.

Cephalotaxus is a small genus of 8–12 species in the monotypic family Cephalotaxaceae (Fu et al. 1999; Hao et al. 2008). *Cephalotaxus harringtonia* (Forbes) K. Koch is a dioecious, evergreen shrub or small tree native to Japan and northeastern China and Korea (Tripp 1995). The Conifer Society (Conifer Society 2018) reports that the species is hardy in North America to zone 7 (USDA ARS 2018). The species is the most widely-cultivated and variable of the genus (Tripp 1995). It is reported to be deer-resistant (NC State Extension 2018) and shade-tolerant (Missouri Botanical Garden 2018).

Spontaneous plants of *Cephalotaxus harringtonia* were first noted by the author at the New York Botanical Garden (NYBG) about the year 2000. Since then, more spontaneous plants have been noted but were considered waifs since numbers were low and distribution limited (Atha et al. 2016). By 2019, however, the number of individuals had greatly increased and additional plants (Figure 1) were found on adjacent property at the Wildlife Conservation Society (Bronx Zoo), prompting this report.

Voucher specimens. New York. Bronx Co.: New York City, New York Botanical Garden, 40°51'22"N, 73°52'37"W, 10 m elev., 8 Apr 2008, *Nee 59042* (NY); New York Botanical Garden, 40.856977, -73.878288, 10 m elev, 22 Mar 2009, *Atha 6914* (NY).

A total of sixty-five spontaneous plants were found within an area of about 121 hectares (300 acres). The ecological communities in which plants were found include (after Edinger et al. 2014) Floodplain Forest Oak Tulip Tree Forest, and Rich Mesophytic Forest. Not every square meter of the area was surveyed, so there could be more plants within the area as well as outside of it. Spontaneous plants range in age from saplings in the first couple of years of growth to large, mature specimens approximately 10 cm diameter and 3–4 m tall. All of the larger plants are apparently males bearing pollen cones most of the year. No spontaneous females were found.

The species is not reported to spread vegetatively, indicating that the dispersal units are the arillate seeds. As the fruit are quite large, mammals are hypothesized to consume the fruit and defecate the seeds. Shade tolerance, deer resistance, and animal dispersal are common traits of aggressive woodland invaders. Based on the behavior of the plants in the Bronx and the wide geographic tolerance reported in the literature, it appears that the species could spread across wooded areas of eastern North America.

Figure 1. *Cephalotaxus harringtonia,* A–D of a single spontaneous individual photographed in Bronx Park, New York City, January 2019. A. Shrub showing multiple stems. B. Trunk about 5 cm diam. C. Top of branch showing lustrous dark green needles and mostly dichotomous twig branching. D. Underside of branch showing whitened needle abaxials and nearly mature, spherical male cones. A–D., <https://www.inaturalist.org/observations/19661181>.

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A NEW COMBINATION IN *LUPINUS SULPHUREUS* (FABACEAE)

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ABSTRACT

The new combination **Lupinus sulphureus** Douglas var. **bingenensis** (Suksd.) Gandhi & Vincent is made here to accommodate *L. bingenensis* Suksd. and *L. bingenensis* var. *subsaccatus* Suksd. at varietal rank in *L. sulphureus*, necessitated by the priority of the varietal autonym *L. bingenensis* var. *bingenensis* from 1923.

The genus *Lupinus* L. (Fabaceae), commonly known as lupin or lupine, has about 220 species (Mabberley, 2017: 544), and its center of diversity is in the New World, with a small number of species occurring in the Mediterranean and tropical African highland regions. Approximately 90 *Lupinus* species are known to occur in the USA (Isely 1998).

Suksdorf (1923: 12–13) published, among others, the new species *Lupinus bingenensis* Suksd. and its var. *subsaccatus* Suksd. As per Article 26.3, the legitimate varietal name *L. bingenensis* var. *subsaccatus* automatically created the autonym *L. bingenensis* var. *bingenensis* (in 1923). Smith (1924: 305) added a new varietal name: *L. bingenensis* var. *dubius* C.P. Sm. Subsequently, Suksdorf (1927: 24) published two more varietal names in *L. bingenensis*: var. *albus* Suksd. and var. *roseus* Suksd.

Smith (1939) described several new varieties in *Lupinus* (including *L. sericeus* Pursh var. *egglestonianus* C.P. Sm.). He (pp. 111–112) transferred *L. bingenensis* and its var. *dubius* to *L. leucopsis* J. Agardh at the rank of variety and made the two new combinations, viz., *L leucopsis* var. *bingenensis* (Suksd.) C.P. Sm. and var. *dubius* (C.P. Sm.) C.P. Sm.

For the forthcoming volume of *Flora of North America North of Mexico* on Fabaceae, the above varietal names are being treated, along with *Lupinus sericeus* Pursh var. *egglestonianus* C.P. Sm. (Smith, 1939: 104) as representing a single taxon at the rank of variety in *L. sulphureus* Douglas ex Hooker. In this regard, the priority of the varietal names is analyzed below.

It is evident from the dates of the varietal names that two varietal names have priority over others, viz., *Lupinus bingenensis* var. *subsaccatus* and the autonym *L. bingenensis* var. *bingenensis* (both created in 1923).

According to the Shenzhen Code (International Code of Nomenclature for Algae, Fungi, and Plants (ICNAFP)) Article 11.6, an autonym has priority over the name at the same rank that established it (Turland et al. 2018: 36). This rule determines the correct name when *Lupinus bingenensis* Suksd. and *L. bingenensis* var. *subsaccatus* Suksd. are treated together as one taxon at the rank of variety in *L. sulphureus*.

Since the varietal autonym *Lupinus bingenensis* var. *bingenensis* has priority over *L. bingenensis* var. *subsaccatus*, the correct varietal name in *L. sulphureus* must be *L. sulphureus* var.

bingenensis. Application of the Code necessitates a new combination at the rank of variety in *L. sulphureus* as *L. sulphureus* var. *bingenensis*. Accordingly, the combination is made here.

LUPINUS SULPHUREUS Douglas var. **BINGENENSIS** (Suksd.) Gandhi & Vincent, **comb. & stat. nov.** *Lupinus bingenensis* Suksd., Werdenda 1: 12. 1923. *Lupinus bingenensis* Suksd. var. *bingenensis* (autonym created in Werdenda 1: 13. 1923). *Lupinus leucopsis* J. Agardh var. *bingenensis* (Suksd.) C.P. Sm., Spec. Lupinorum 112. 1939. **LECTOTYPE** (designated by C.P. Smith, Spec. Lupinorum 112. 1939): **USA. Washington**, Klickitat Co.: Zwischen zerstreuten Baumen an einem trockenen Hugel bei Bingen, 24 Apr, 12 Jun 1905, *W.N. Suksdorf 5036* (WS; isolectotypes: CAS!, DAO!, GH!, K!, NY!, OSC!, PH!, US!, WTU). Note: both dates are printed on the label.

Lupinus bingenensis var. *subsaccatus* Suksd., Werdenda 1: 13. 1923. *Lupinus sulphureus* var. *subsaccatus* (Suksd.) C.L. Hitchc. in C.L. Hitchcock et al., Vasc. Pl. Pacif. N. W. 3: 330. 1961. **LECTOTYPE** (here designated): **USA. Washington.** Klickitat Co.: Sie Wurde am steilen, sonnigen Abhang oben am Bingenberge (etwa 600 m), bei Bingen gesammelt, 25 May 1923, *W.N. Suksdorf 11405* (WS; isolectotypes: BM!, GH!, OSC!, PH!, RSA!, US!, WTU).

Lupinus bingenensis var. *dubius* C.P. Sm., Bull. Torrey Bot. Club 51: 305. 1924. *Lupinus leucopsis* var. *dubius* (C.P. Sm.) C.P. Sm., Spec. Lupinorum 111. 1939. **TYPE**: **USA. Washington.** Benton Co.: Prosser, 27 May 1903, *J.S. Cotton 1106* (holotype: WS).

Lupinus bingenensis var. *albus* Suksd., Werdenda 1: 24. 1927. **LECTOTYPE** (here designated): **USA. Washington.** Klickitat Co.: *s.d.*, *W.N. Suksdorf 10191* (WS; isolectotypes: BM!, GH!, PH!, RM!, RSA!, US!, WTU).

Lupinus bingenensis var. *roseus* Suksd., Werdenda 1: 24. 1927. **LECTOTYPE** (here designated): **USA. Washington.** Klickitat Co.: *s.d.*, *W.N. Suksdorf 11855* (WS; isolectotypes: BM!, RSA!, US!, WTU).

Lupinus sericeus Pursh var. *egglestonianus* C.P. Sm., Spec. Lupinorum 104. 1939. **TYPE**: **USA. Oregon.** Sherman Co.: Grass Valley, *s.d., C.P. Smith 35127* (holotype: DS, housed at CAS; isotypes: CAS, DAO!, UMO).

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AIRA ELEGANS (POACEAE) AND *MEDICAGO ORBICULARIS* (FABACEAE): NEW TO THE KENTUCKY FLORA

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ABSTRACT

Aira elegans Willd. (Poaceae) and *Medicago orbicularis* (L.) Bartal. (Fabaceae), two annuals native to Eurasia and North Africa, are documented here as new to the flora of Kentucky.

During field surveys in Calloway Co., Kentucky, we discovered *Aira elegans* (Poaceae) in 2013 and *Medicago orbicularis* (Fabaceae) in 2015. Collection sites for both are located within the Gulf Coastal Plain (Jackson Purchase region) of southwestern Kentucky (Figure 1). Neither species has previously been documented for Kentucky, based on recent floras, manuals, and atlases (Brown & Athey 1992; Medley 1993; Jones 2005; Wipff 2007; Campbell & Medley 2014; Kartesz 2015; Weakley 2015; NatureServe 2019; USDA, NRCS 2019).

AIRA ELEGANS Willd. (annual silver hairgrass)

We initially found annual silver hairgrass in an unmown lawn and subsequently discovered another population 0.5 km east of the first population site along a weedy roadside. Although treating it as *A. caryophyllea* L. var. *capillaris* (Mert. & W.D.J. Koch) Mutel., Wipff (2007) pointed out that *A. elegans* Willd. is the correct binomial at species rank but erroneously reported the authorship as Willd. ex. Roem. & Schult. Roemer & Schultes credit the name and description to Willdenow, so they should not be part of the authorship. *Aira elegantissima* Schur, presently considered a heterotypic synonym of *A. elegans* (Weakley 2015; Univ. of Tennessee Herbarium 2019), is rarely applied in other treatments (see Kartesz 2015).

Voucher specimens. USA. Kentucky. Calloway Co.: Murray, 1405 Lancaster Road (KY 497) at jct of Emma Drive, unmown lawn with a weedy component of annual/perennial naturalized taxa, elev. 150 m, 36.734112°, -88.129391°, infrequent, 6 Jun 2013, *Thompson & Abbott 13-264* (BEREA); Murray, 190 Emma Drive adjacent to Johnny Lane, disturbed roadside edge, elev. 129 m, 36.731154°, -88.123548°, scarce, 8 Jun 2013, *Thompson & Abbott 13-270* (BEREA) (Figure 2). Duplicates of these collections and for the *Medicago* have been sent to APSC, MO, NCU, and UAM.

Common habitats for *Aira elegans* in the USA are open, dry to moist, sandy and rocky loam soils in woodland openings, grassy sunny openings (Wipff 2007), and disturbed soil of pastures, fields, lawns, roadsides, and waste places (Radford et al. 1968; Tucker 1996; Weakley 2015). Associated species are alphabetically recorded here for the sites cited above: *Agrostis hyemalis, Arenaria serpyllifolia, Coreopsis tinctoria, Daucus carota, Dichanthelium laxiflorum, Krigia caespitosa, Kummerowia striata, Plantago lanceolata, Schedonorus arundinceus, Sherardia arvensis, Taraxacum officinale, Trifolium campestre, T. pratense*, *Triodanis perfoliata,* and *Vulpia octoflora.*

In Stewart County, near Dover in northwestern Tennessee, we documented *Aira elegans* in a sunny, open upland successional old field, 15 June 2015. At this site, annual silver hairgrass was commonly associated with *Bromus japonicus, Daucus carota, Dianthus armeria, Kummerowia striata, Phleum pratense, Plantago aristata, Schedonorus arundinaceus, Trifolium campestre*, and *Vulpia octoflora.* University of Tennessee Herbarium (2019) documents the occurrence of *Aira elegans* in 13 Tennessee counties.

Voucher specimen. USA. **Tennessee.** Stewart Co.: Dover, Keel Spring Nature Trail, mesophytic hardwood forest, 7.0 km S on TN 943 (Leatherwood Road) from jct US 79, White Oak Trail on Bluegrass Ridge in old field upland successional forest, elev. 175 m, 36.438477°, -87.862221°, frequent, 15 Jun 2015, *Thompson & Abbott 15-424* (BEREA).

In addition to *Aira elegans*, two other species of *Aira*, *A. caryophyllea* and *A. praecox*, have been documented in the southeastern Atlantic USA and the western Pacific USA. *Aira elegans* may be separated by pedicels 2–8x as long as the 1.7–2.5 mm spikelet; and has two florets with the uper lemma with an 1.5–2.5 mm awn and the lower floret awnless or minutely awned (Wipff 2007; Weakley 2015). Other vernacular names for the species include delicate hairgrass, elegant hairgrass, Mediterranean hairgrass, and silver hairgrass (Wipff 2007; Weakley 2015; GBIF 2017; Mifsud 2019; USDA, NRCS 2019).

The native geographical range of *Aira elegans* includes southeastern Europe, northern Africa, and western Asia. It has become naturalized throughout Eurasia, eastern and southern Africa, Australia, New Zealand, temperate South America, Japan, Korea, and the eastern and western USA (Tucker 1996; Wipff 2007; GBIF 2017).

Hitchcock (1950) reported *Aira elegans* in 13 states during the 1950s. It is presently known from 18 states, ranging from New Jersey southward through the Gulf Coastal Plain west to New Mexico, California, Oregon, and Washington (Kartesz 2015; USDA, NRCS 2019). NatureServe (2019) cites 20 states including Hawaii and West Virginia.

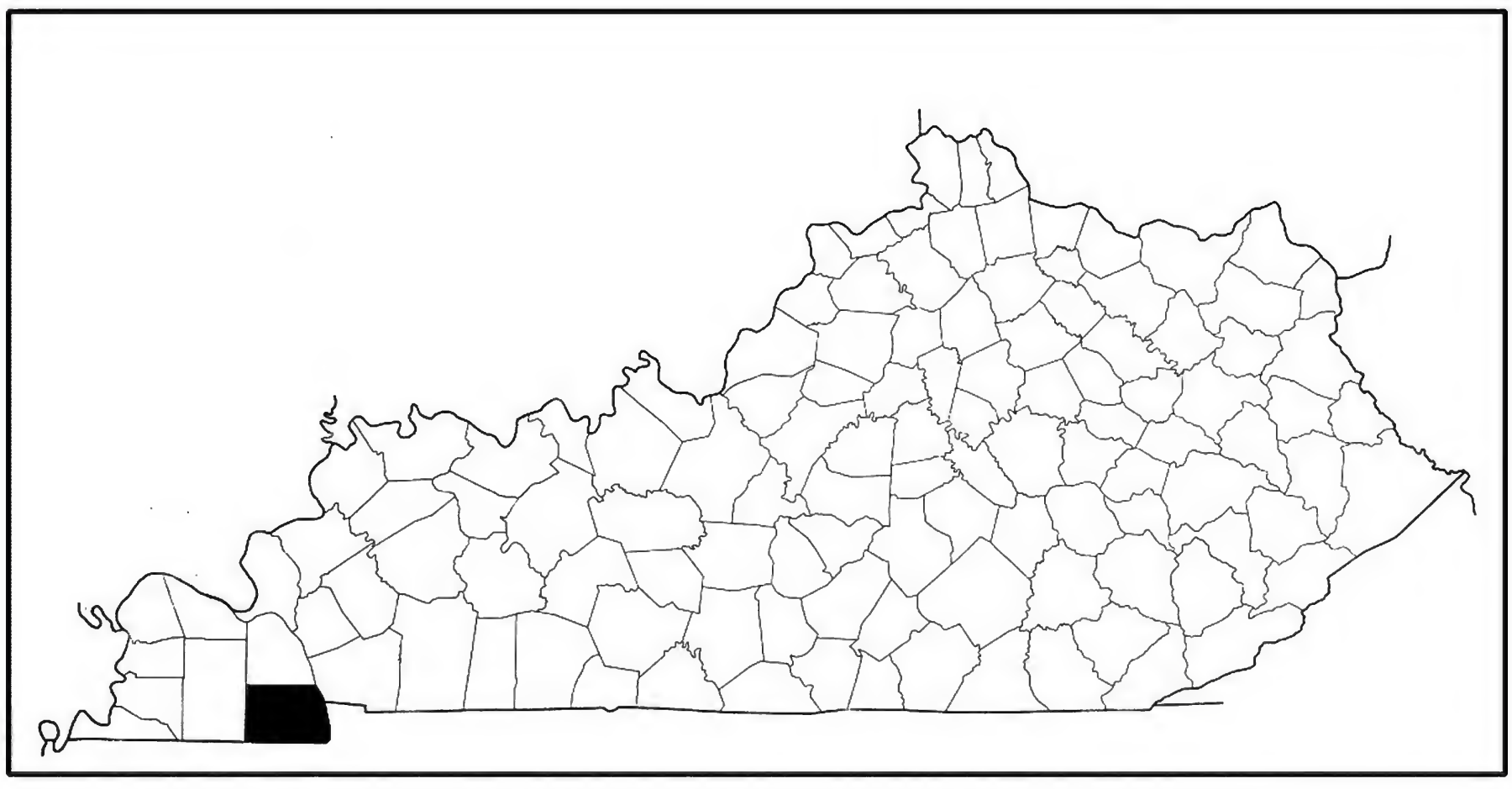

Figure 1. Calloway Co., Kentucky, within the Gulf Coastal Plain contiguous to Tennessee.

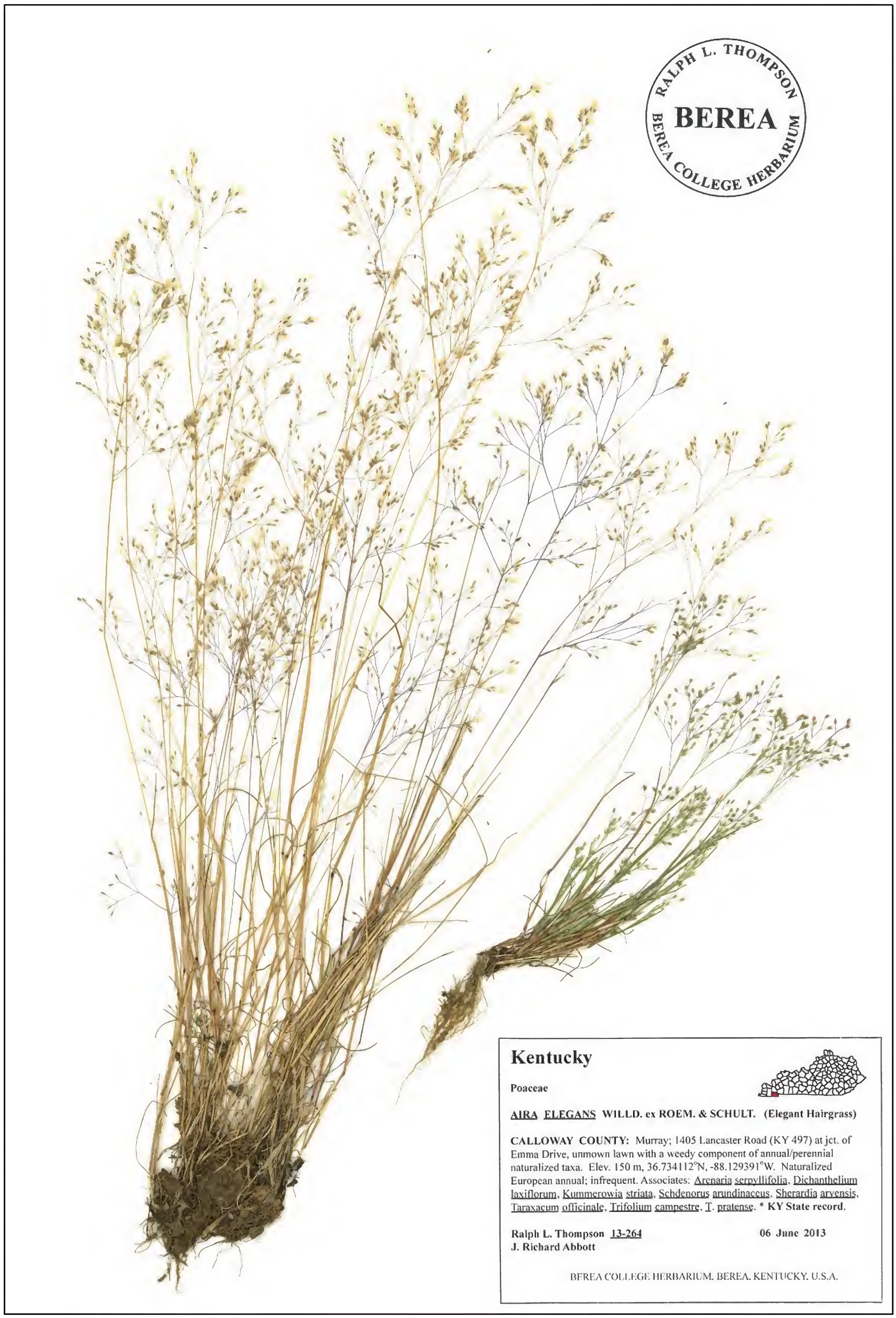

Figure 2. *Aira elegans* from Calloway Co., Kentucky (*Thompson & Abbott 13-264*, BEREA).

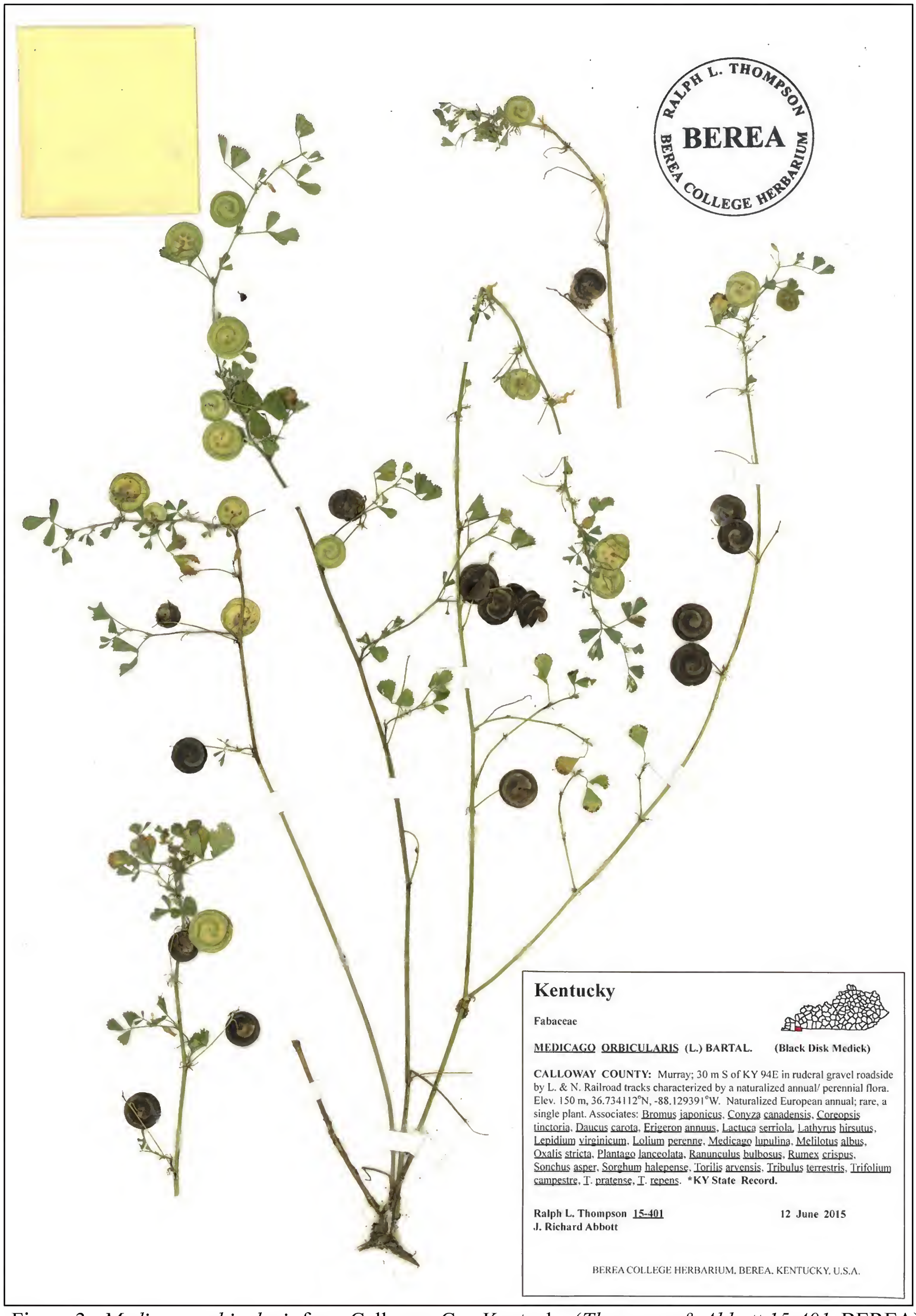

Figure 3. *Medicago orbicularis* from Calloway Co., Kentucky (*Thompson & Abbott 15-401*, BEREA).

MEDICAGO ORBICULARIS (L.) Bartal. (button medic)

We document this species as new to Kentucky from a single procumbent, mat-forming plant at a gravel roadside adjacent to the Louisville & Nashville Railroad right-of-way.

Voucher specimen. USA. Kentucky. Calloway Co.: Murray; 30 m S of KY Hwy 94E, gravel roadside along Louisville & Nashville Railroad tracks, elev. 150 m, 36.734112°, -88.129391°, rare, one plant, 12 Jun 2015, *Thompson & Abbott 15-401* (BEREA). Figure 3.

At the collection site, 17 of 23 associates are naturalized European or Asian taxa: *Bromus japonicus, Conyza canadensis, Coreopsis tinctoria, Daucus carota, Erigeron annuus, Lactuca serriola, Lathyrus hirsutus, Lepidium virginicum, Lolium perenne, Medicago lupulina, Melilotus albus, Oxalis stricta, Plantago lanceolata, Ranunculus bulbosus, Rumex crispus, Sonchus asper, Sorghum halepense, Torilis arvensis, Tribulus terrestris, Trifolium campestre, T. pratense,* and *T. repens*.

Medicago orbicularis, a glabrous, procumbent or mat-forming annual, may be separated from other *Medicago* taxa by its large spineless, papery, discoid-orbicular, 3–5-spirally-coiled tan legumes, and very deeply laciniate-lacerate stipules (Isley 1990, 1998; Weakley 2015; Woods & Orcuff 2017; Mifsud 2019). Habitats for button medic in the USA include sandy and calcareous roadsides, railroad right-of-ways and ballast, agricultural fields, meadow, and pastures, vacant lots, lawns, and abandoned waste ground (Radford et al. 1968; Isley 1990, 1998; Weakley 2015; Woods & Orcuff 2017). Vernacular names for *Medicago orbicularis* include blackdisc clover, blackdisc medic, burless clover, burless trefoil, button burclover, button clover, button medic, button trefoil, disc medic, flat snail clover, large-disc medic, and round-fruited medic (GBIF 2017; Mifsud 2019).

Within the continental USA, *Medicago orbicularis* has been reported as introduced and/or naturalized in Alabama, California, Florida, Georgia, Illinois, Louisiana, Maryland, Mississippi, New Jersey, North Carolina, Oklahoma, Tennessee, and Texas (NatureServe 2019; USDA, NRCS 2019). Kartesz (2015) also mapped it for Arkansas. University of Tennessee Herbarium (2019) mapped it in eight Tennessee counties. Woods & Orcuff (2017) mapped button medic in seven Alabama counties and presented an extensive taxonomic treatment including keys, descriptions, synonymy, county maps, and herbarium specimen photos.

Medicago orbicularis is native to Mediterranean Eurasia and North Africa (Isley 1990, 1998). Lesins & Lesins (1979) stated the eastern Mediterranean Basin is the center for diversity of the genus *Medicago*. Mifsud (2019) reported a broad geographical distribution of *M. orbicularis* in the Mediterranean Basin and Middle Europe, the Middle East, North Africa, and the major Mediterranean Islands. Button medic has been introduced to Australia, South America, northern and eastern Africa, and the eastern and western USA (GBIF 2017; Mifsud 2019).

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RECONSIDERING NORTHERN AND SOUTHERN TAXA OF ISLAND MALLOW (*MALVA ASSURGENTIFLORA*, MALVACEAE) AND THEIR CONSERVATION STATUS ON THE CALIFORNIA CHANNEL ISLANDS

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ABSTRACT

Phylogenetic analyses of molecular sequence data since the mid-1990s have demonstrated the non-monophyly of *Lavatera* and *Malva* (Malvaceae) as treated earlier and have resulted in the taxonomic rearrangement of these genera so that each is reciprocally monophyletic. During this recircumscription, four taxa from western North America previously recognized in *Lavatera* were transferred to *Malva*, but new combinations for the subspecies of *L. assurgentiflora* were not made. Here, based on the morphological distinctiveness of those infraspecific taxa, the new combination **Malva assurgentiflora** subsp. **glabra** (Philbrick) Guilliams, **comb. nov.**, is made for plants from San Clemente and Santa Catalina islands. Re-evaluation of the native and introduced distributions of subsp. *assurgentiflora* and subsp. *glabra* indicates that both taxa are exceedingly rare in native occurrences and warrant continued conservation attention.

Phylogenetic analyses of molecular sequence data often provide critical and decisive evidence for realignment of organismal classifications so that taxonomy reflects evolutionary history. This is especially true for difficult taxonomic groups with competing classification schemes based on morphological evidence, as is the case in the *Malva* alliance (Malvaceae, tribe Malveae; Bates 1968). Comprising the Linnean genera *Alcea*, *Althaea*, *Lavatera*, and *Malva*, the *Malva* alliance has been the subject of a number of molecular phylogenetic studies (Ray 1995; Fuertes-Aguilar et al. 2002; Escobar García et al. 2009). The first of these studies (Ray 1995) demonstrated the non-monophyly of both *Lavatera* and *Malva*, leading Ray (1998) to reassign subordinate taxa between these genera so that each is reciprocally monophyletic. Thorough discussions, including of the morphology of these plants, can be found in the studies cited above.

While the *Malva* alliance has a main center of diversity in western Europe and the Mediterranean region, a small, but intriguing cluster of taxa is native to the California Islands off the coast of western North America (Figs. 1, 2). In the USA, *M. assurgentiflora* (Kellogg) M.F. Ray [*Lavatera assurgentiflora* Kellogg] occurs naturally on four of the eight California Channel Islands at the present time. In México, three currently recognized taxa are considered native to the Baja California Pacific Islands, including *M. lindsayi* (Moran) M.F. Ray [*Lavatera lindsayi* Moran], *M. occidentalis* (S. Wats.) M.F. Ray [*Lavatera occidentalis* S. Wats.], and *M. pacifica* M.F. Ray [*Lavatera venosa* S. Wats.]. These native North American taxa are shrubby perennials, a life history feature that is convergent with a number of Old World *Malva* alliance taxa in both the Core Malvoid clade as well as the *Lavatera* clade. The shrub habit may have evolved from the herbaceous perennial habit up to six times in the *Malva* alliance (Escobar García et al. 2009).

The early phylogenetic work that resulted in the transfer of native North American *Malva* alliance taxa from *Lavatera* to *Malva* (Ray 1995, 1998) had an additional effect with respect to *Malva assurgentiflora*: the loss of available names for infraspecific taxa. Philbrick (1980) provided morphological evidence for the recognition of two subspecies in (then) *L. assurgentiflora* across its

range on the California Channel Islands. Philbrick observed that northern Channel Island plants from San Miguel and Anacapa islands differ from plants from the southern Channel Islands of San Clemente and Santa Catalina in having pubescent leaves with stellate trichomes, entire petal apices, and pubescent filament columns (Figs. 3, 4). Southern Channel Island plants, which he recognized as subsp. *glabra*, have glabrous leaves, erose petal apices, and glabrous filament columns.

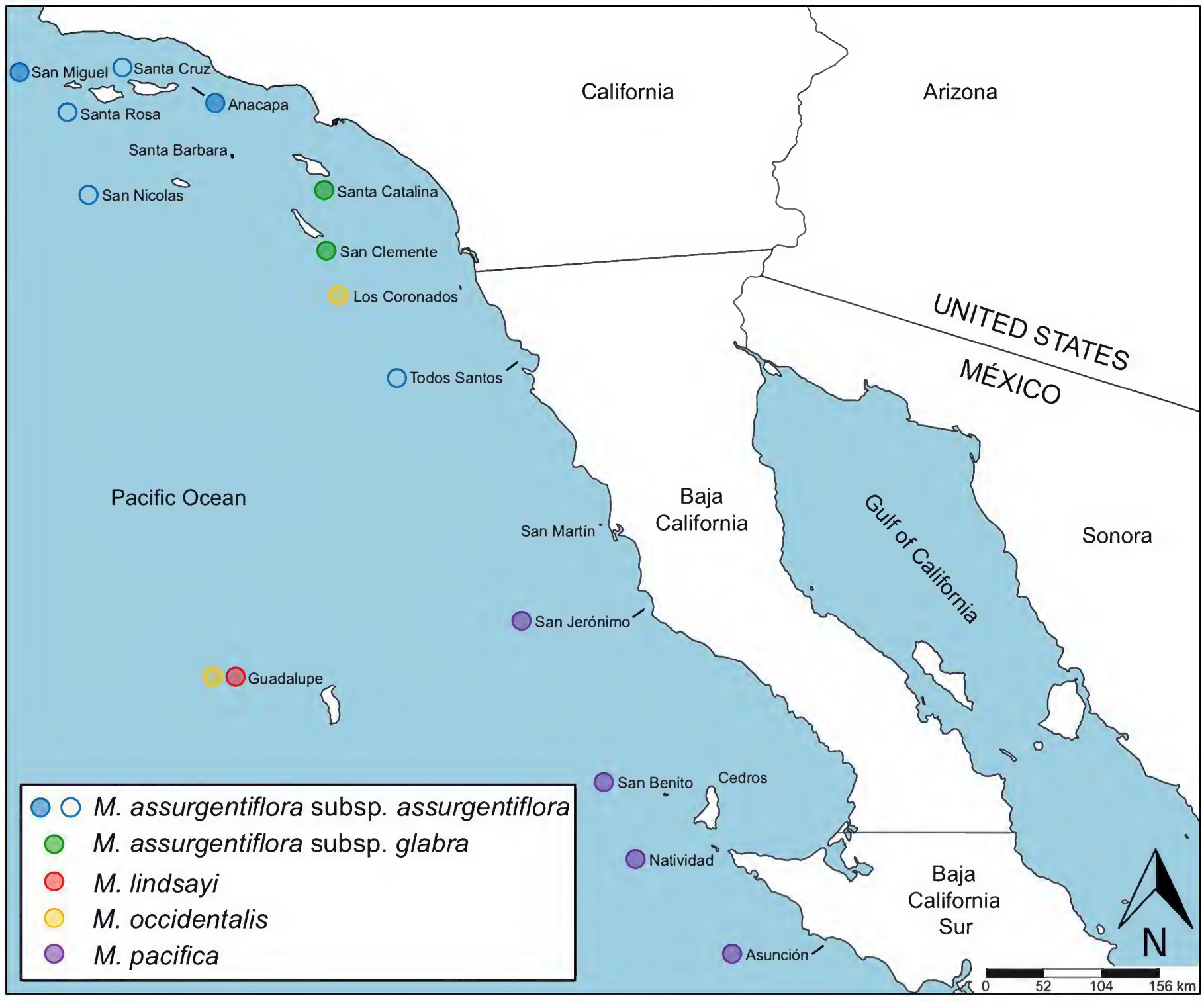

Figure 1. Map of the California Islands of the southwestern United States and northwestern México. Islands on which western North American *Malva* taxa occur are indicated with colored circles. Circles are filled when a taxon is considered naturally occurring on an island, and unfilled when considered introduced.

Despite the clear morphological differences between the *Lavatera assurgentiflora* subspecies, Philbrick's taxonomic distinction has not been broadly adopted beyond local botanical experts of the Channel Islands. His concept was not followed in the Jepson Manual treatment of *Lavatera* (Hill 1993), although the treatment author later suggested that further study might result in recognition of two taxa in *M. assurgentiflora* (Hill 2009). Similarly, Ray did not make new combinations for subsp. *assurgentiflora* and subsp. *glabra* in *Malva* in his 1998 paper. Ray did describe the morphological distinctiveness of the two subspecies, however, providing additional characters that distinguish them and noting that these features were maintained when plants are grown in a common garden (Ray 1998). Ostensibly due to the strength of the morphological evidence and its genetic basis, in 1996 Ray annotated the type specimens of both subspecies with new combinations in the genus *Malva*

(Figs. 5 and 6). Ultimately, however, Ray (1998) decided against validly publishing new combinations, indicating that a more thorough field investigation was necessary to determine the provenance of a plant collected on Santa Cruz Island (a northern Channel Island) that he considered to be morphologically consistent with the southern island subspecies (*Junak SR-1847*, SBBG).

Figure 2A-F. Photographs of island endemic *Malva* taxa of western North America. A. *Malva assurgentiflora* subsp. *assurgentiflora* [*Lavatera assurgentiflora* subsp. *assurgentiflora*], showing plant habit, photograph by E.R. Blakley. B. *Malva assurgentiflora* subsp. *assurgentiflora*, leaves and flowers, photograph by Ralph N. Philbrick. C. *Malva assurgentiflora* subsp. *glabra* [*Lavatera assurgentiflora* subsp. *glabra*], leaves and flowers, photograph by Dieter H. Wilken. D. *Malva lindsayi* [*Lavatera lindsayi*], leaves and flowers, photograph by Steven Junak. E. *Malva occidentalis* [*Lavatera occidentalis*], flowers and fruits, photograph by Steven Junak. F. *Malva pacifica* [*Lavatera venosa*], leaves and flowers, photograph by Steven Junak.

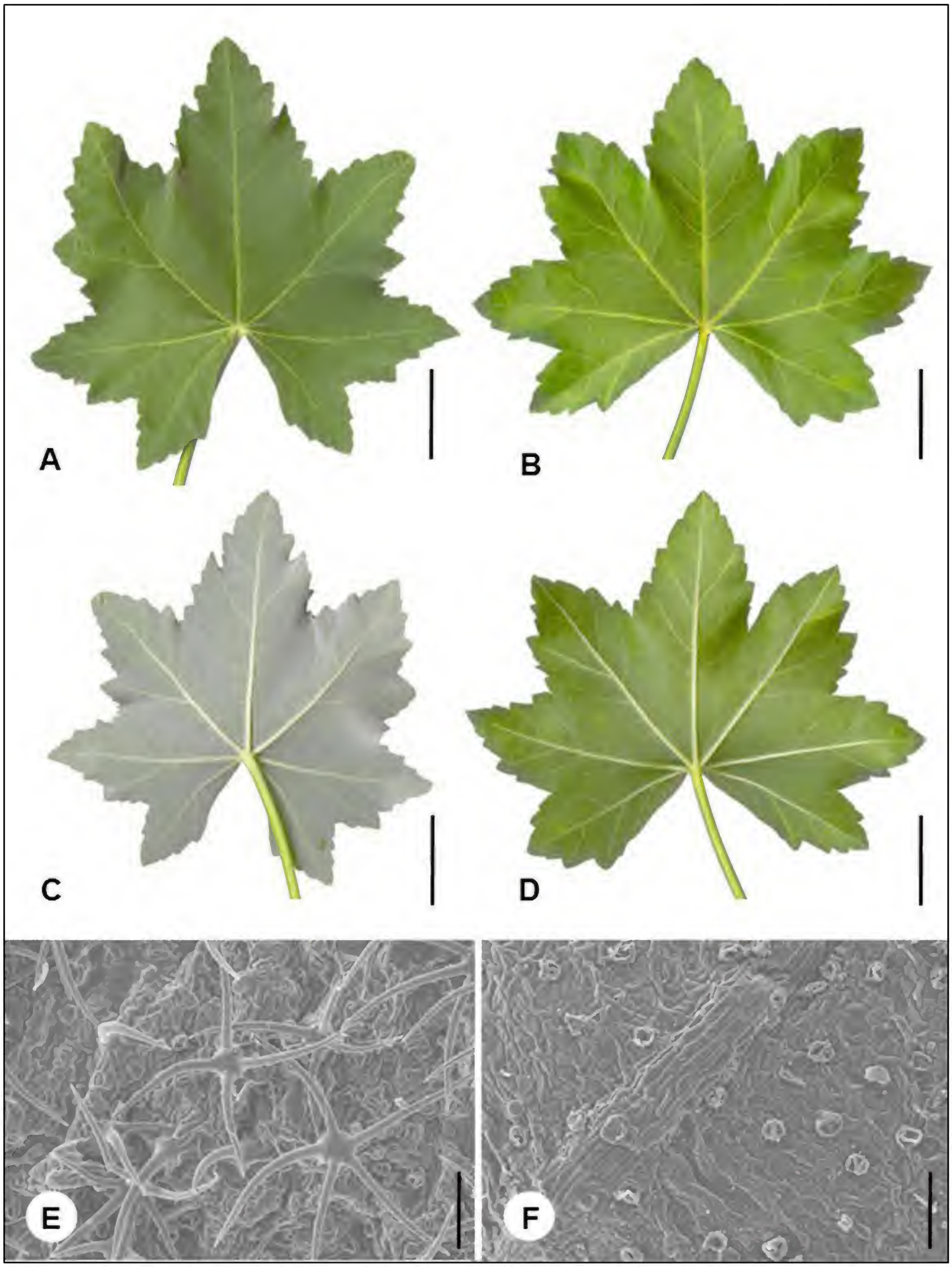

Figure 3A-F. Photographs and scanning electron microscope images of leaves of *Malva assurgentiflora*. A. *M. assurgentiflora* subsp. *assurgentiflora*, adaxial leaf surface, scale bar = 3 cm. B. *M. assurgentiflora* subsp. *glabra*, adaxial leaf surface, scale bar = 3 cm. C. *M. assurgentiflora* subsp. *assurgentiflora*, abaxial leaf surface, scale bar = 3 cm. D. *M. assurgentiflora* subsp. *glabra*, abaxial leaf surface, scale bar = 3 cm. E. Scanning electron microscope image of *M. assurgentiflora* subsp. *assurgentiflora*, adaxial leaf surface, scale bar = 100 μM. F. Scanning electron microscope image of *M. assurgentiflora* subsp. *glabra*, adaxial leaf surface, scale bar = 100 μM.

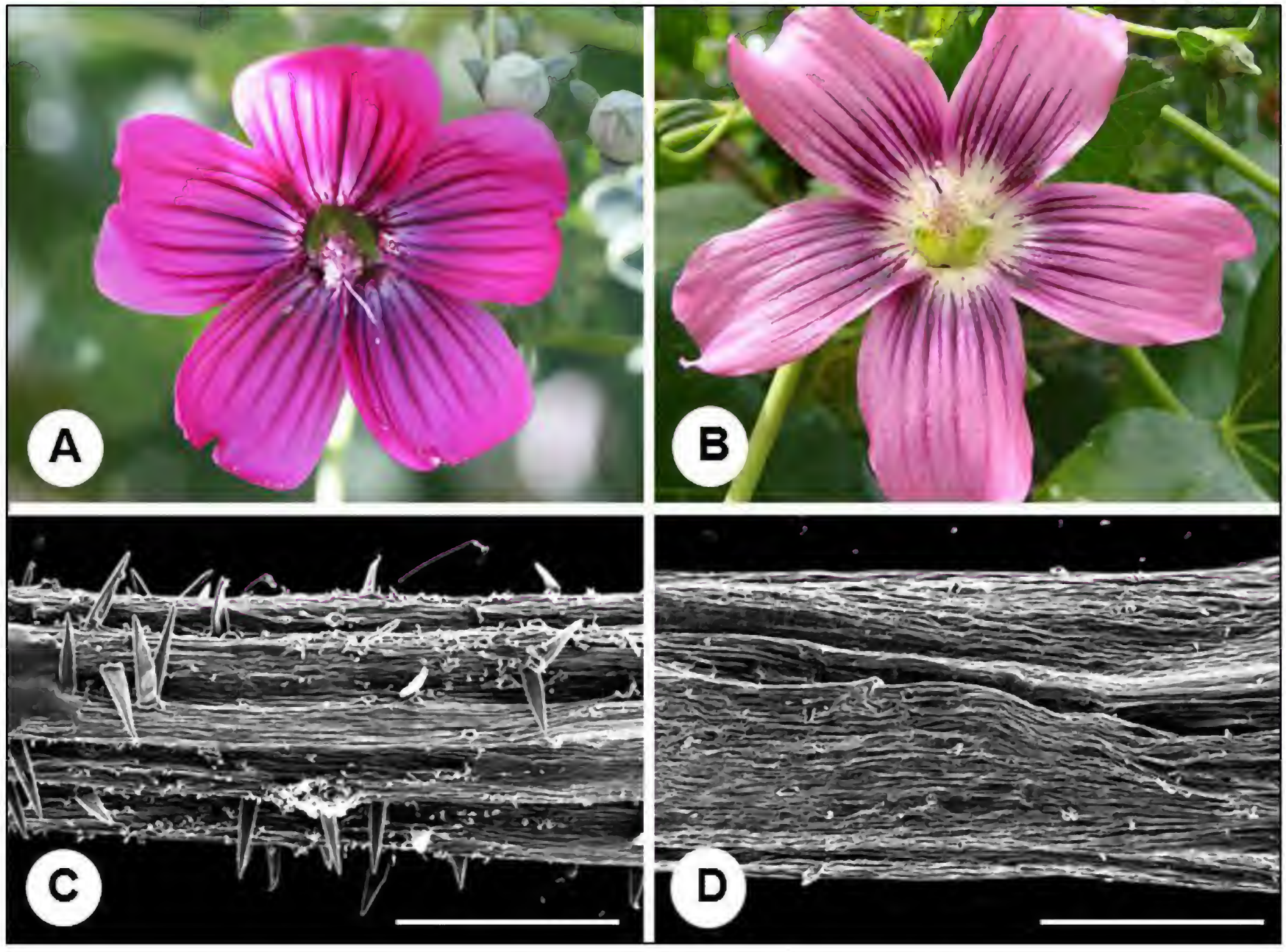

Figure 4A-B. Photographs of flowers and scanning electron microscope images of filament columns of *Malva assurgentiflora*. A. *M. assurgentiflora* subsp. *assurgentiflora*, flower, photograph by Sally Isaacson. B. *M. assurgentiflora* subsp. *glabra*, flower, photograph by Tricia Wardlaw. C. *M. assurgentiflora* subsp. *assurgentiflora*, filament column, scale bar = 500 µM. D. *M. assurgentiflora* subsp. *glabra*, filament column, scale bar = 500 µM.

Current floristic work across the California Channel Islands has permitted an evaluation of Philbrick's taxonomic treatment of *Malva assurgentiflora*. Study of the species across its natural and introduced range was performed. Strong morphological patterns consistent with Philbrick's taxonomy are clear, and therefore nomenclature must be updated so that plant diversity across the California Channel Islands can be adequately described in upcoming regional floras. Here, a new combination is provided for *Lavatera assurgentiflora* subsp. *glabra* in the genus *Malva*. Also given is a summary of the distribution of the northern subspecies of *M. assurgentiflora* [*L. assurgentiflora* subsp. *assurgentiflora*], which has a broad, introduced range owing to its widespread usage in horticulture. Finally, a brief section on implications for conservation is provided.

Methods

This paper is based upon the analysis of *Malva assurgentiflora* [*Lavatera assurgentiflora*] by Philbrick (1980), the careful description of the species by Ray (1998), and recent examination of *M. assurgentiflora* in the field and herbarium. Fieldwork for this project was performed in 2015–2017. A list of herbarium specimens examined is provided. Living, wild-collected plants in cultivation and digital images available online were examined. Critical to establishing an accurate understanding of the present-day distribution of the species were direct conversations with island experts Michael Benedict, Sarah Chaney, Elizabeth Collins, Dr. Robert DeLong, Peter Dixon, Steven Junak, John Knapp, Julie Lambert, Dr. Ralph Philbrick (now deceased), Dirk Rodriguez, and Ian Williams.

MALVA ASSURGENTIFLORA Kellogg **subsp. GLABRA** (Philbrick) Guilliams, **comb. nov. Basionym:** *Lavatera assurgentiflora* subsp. *glabra* Philbrick, The California Islands: Proceedings of a Multidisciplinary Symposium, 177. 1980. **TYPE: USA. California.** Los Angeles Co.: Santa Catalina Island, Bird Rock, 23 Sep 1961, *E.R. Blakley 4739* (holotype: SBBG!; isotype: CAS). Figure 5.

Figure 5. Holotype of *Malva assurgentiflora* subsp. *glabra* (*Blakley 4739*; current catalog number SBBG150066; old catalog number 12937).

Figure 6. Neotype of *Malva assurgentiflora* subsp. *assurgentiflora* (*Timbrook & Philbrick 652*; current catalog number SBBG150065, old catalog number 87733). Material from Kellogg unequivocally corresponding to holotype of *Lavatera assurgentiflora* could not be located by Ray (1998), thus this neotype was designated by Ray (1995).

Malva assurgentiflora subsp. *glabra* is morphologically distinctive. With its green, shiny, glabrous leaves, subsp. *glabra* can be confidently distinguished at a distance from subsp. *assurgentiflora*, with gray-green, dull, stellate pubescent leaves. The subspecies also differ strongly in floral features. In all material examined, subsp. *glabra* has oblong or oblanceolate to narrowly obtriangular petals with an erose apex; subsp. *assurgentiflora* has obovate to obtriangular petals with an entire apex. As noted by Philbrick, the filament column of subsp. *glabra* is also usually glabrous, while in subsp. *assurgentiflora* it is usually pubescent. In these features, the specimen of putative subsp. *glabra* collected on Santa Cruz Island (*Junak SR-1847*) is more consistent with subsp. *assurgentiflora*, although the leaves are less pubescent than is typical for the subspecies.

Although an attractive plant, subsp. *glabra* is not widely used in the horticultural trade at the present time, perhaps owing to the early introduction of subsp. *assurgentiflora*, described below. Both subspecies grow vigorously in cultivation, however, and all plants observed of both subspecies grown at the Santa Barbara Botanic Garden maintain the diagnostic morphological features described by Philbrick (1980), Ray (1998), and above (Guilliams, personal observation).

The global distribution of *Malva assurgentiflora* subsp. *assurgentiflora*

Malva assurgentiflora subsp. *assurgentiflora,* originally collected from Anacapa Island, is widely used in the horticultural trade. One early reference to the horticultural use of subsp. *assurgentiflora* was made by Behr (1891), who observed the plant in a garden setting in San Francisco, California in September 1850. By 1854, Behr (1891) observed the plant increasingly in use as a garden hedge, and Kellogg (1854) wrote in the protologue (for *Lavatera assurgentiflora*) that it was "now to some extent cultivated." Philbrick (1980) noted that the plant was cultivated as far south as Ecuador by 1918. Today, in the Western Hemisphere, subsp. *assurgentiflora* has been planted in Bolivia, Chile, Columbia, Ecuador, Mexico, Peru, and the United States. The subspecies has also potentially naturalized in Australia and New Zealand (Barker 1977; Allan Herbarium 2000).

Malva assurgentiflora subsp. *assurgentiflora* has also been planted in horticultural settings on the California Channel Islands. An overview of the current distribution of subsp. *assurgentiflora* on each California Channel Island is given below. For information on historical observations of subsp. *assurgentiflora* on the Channel Islands, see Philbrick (1980). Islands are discussed in order, from the northwest to the southeast.

San Miguel Island is the northwestern-most island in the archipelago, and one of two islands on which subsp. *assurgentiflora* is known to be naturally occurring at the present time. Three or four individuals of a larger historical occurrence grow in a natural setting near Point Bennett, the westernmost point of the island. Other individuals from this population were transplanted to two higher positions nearby, where an unknown number (10s) of plants remain today (R. DeLong, personal communication). One potentially naturally occurring plant was observed on the east end of the island, in a natural setting, near Willow Canyon. The National Park Service also has planted 15 individuals on the mesa, grown from seed collected on-island.

On Santa Rosa Island, two plants of subsp. *assurgentiflora* occur together near the bunkhouse at the former Vail Ranch, at Bechers Bay. Island biologists Michael Benedict, Steven Junak, Ken Niessen, and Ralph Philbrick, each with long histories on the northern Channel Islands, corroborate the location of these plants and their presumed status as planted in this location in a human settlement. Where these two plants came from originally is unclear, but there is no record of collections of *M. assurgentiflora* from a natural setting on Santa Rosa Island. Therefore, lacking other information, it must be concluded that the species does not occur there naturally at the present time.

On Santa Cruz Island, plants of subsp. *assurgentiflora* were known to occur in only a few regions. A single, large plant grew in the fenced front yard of the ranch house at Christy Ranch on the west end of the island (Michael Benedict, personal communication). This plant was already fully mature when Benedict first observed it in 1964, so he concluded that it must have been planted some years prior. Its original source is unknown. Plants are also known to be planted in the garden and nearby environs of the Main Ranch in the Central Valley, sometimes referred to as the Stanton Ranch. Benedict believes that they were given to former ranch owner, Carey Stanton, from material obtained from Vail Ranch on Santa Rosa Island. Some plants from the Main Ranch were planted at the nearby University of California Field Station. All of these locations are within or adjacent to human settlements. Junak's collection (*SR-1847*) occurs along a road in the Central Valley, presumably recruited from seed of individuals planted elsewhere in the valley. No plants of subsp. *assurgentiflora* are unequivocally known to be naturally occurring on Santa Cruz Island at the present time.

On Anacapa Island, technically a small island group of three main islets, subsp. *assurgentiflora* has been documented from naturally occurring plants on the West Anacapa and Middle Anacapa islets. Recent searches have failed to relocate these plants, however, and the subspecies is presumed extirpated from these two islands at this time. Prior to its extirpation on Middle Anacapa Island, however, seed was gathered by Junak and National Park Service staff. This seed was used to create a new population of subsp. *assurgentiflora* on East Anacapa Island, where plants are currently tended by the Park and are reported to be thriving.

On San Nicolas Island, subsp. *assurgentiflora* grows near several buildings on the island, as well as in one location in a natural setting to which it has apparently spread since its initial introduction. Most plants occur in "Nicktown", a center of military activity on San Nicolas Island, where many individuals grow among buildings in landscaping beds (Junak 2008; Guilliams, personal observation). Some plants grow nearby (e.g., within meters), outside of planters, and have presumably recruited from seed. Away from Nicktown, plants have been observed near Building 189, off Tufts Road, near Building 182 (the Telemetry Building), and at Hill 819 near an old dwelling. Finally, a small stand of subsp. *assurgentiflora* plants has been observed growing in relatively intact native habitat away from but close to Nicktown, leading Junak (2008) to speculate on their provenance. These plants from the base of the north island escarpment have been included in a recent population genetics study that has shown them to be nearly genetically identical to the Nicktown plants (Guilliams et al. 2018), and are likely derived from seed of the introduced northern island plants at Nicktown.

On San Clemente Island, subsp. *assurgentiflora* individuals were planted near the galley and barracks in the town at Wilson Cove. These northern island plants have reportedly been removed and replaced with plants of subsp. *glabra* grown on San Clemente Island using local seed (Julie Lambert, personal communication).

On Santa Catalina Island, subsp. *assurgentiflora* has been planted in Avalon Canyon (Thorne 1967; Guilliams, personal observation). These landscaping plants are morphologically consistent with plants widely available in the horticultural trade, and individuals grow with other landscaping plants in the town center. Millspaugh and Nuttall (1923) reported that material of subsp. *glabra* from Bird Rock (the type locality of subsp. *glabra*) was planted in Avalon, but no individuals of subsp. *glabra* were observed during fieldwork for this project.

Summary of the geographic distribution of *Malva assurgentiflora* subspecies

At the present time and as described by Philbrick (1980), *Malva assurgentiflora* subsp. *assurgentiflora* appears to grow naturally on San Miguel and Anacapa islands. Observations of this subspecies on other islands are nearly all within or adjacent to human settlements and clearly

represent horticultural plantings in historical times. The only exceptions are (1) on Santa Cruz Island, in the Central Valley (*Junak SR-1847*) and (2) on San Nicolas Island, where one small group of plants grows in a natural setting. On Santa Cruz Island, the plant in question occurs along a roadside in the Central Valley, a region in which subsp. *assurgentiflora* is used horticulturally. On San Nicolas Island, the plants in question have been shown to be nearly genetically identical to individuals deliberately planted within the human settlement there.

Naturally occurring plants of *Malva assurgentiflora* subsp. *glabra* are exclusively found on San Clemente and Santa Catalina islands, where they have a long history of documentation by botanists (Raven 1963; Thorne 1967; Philbrick 1980, and references therein). The plant is rarely used in the horticultural trade and the global distribution of subsp. *glabra* is essentially limited to the California Channel Islands.

Conservation implications

Because of the broad use of *M. assurgentiflora* subsp. *assurgentiflora* in horticulture worldwide, some may have the impression that the native Channel Islands malvas are common. In truth, each subspecies is exceedingly rare in nature.

Malva assurgentiflora subsp. *assurgentiflora* is known from only four or five original, naturally occurring plants in total, all growing on San Miguel Island. On Anacapa, the last observation of naturally occurring subsp. *assurgentiflora* was made in 1994 (Junak, personal communication). These islands, both managed by the National Park Service as part of Channel Islands National Park, have each supported activities designed to create new populations and increase the overall number of plants on each island. On San Miguel Island, three new populations of five individuals each of *M. assurgentiflora* have been established using plants grown from seed collected on-island (Dirk Rodriguez, personal communication). Of these, 10 plants persist today and some are relatively large. Although there are no naturally occurring plants remaining on Anacapa Island and as stated previously, seed from Middle Anacapa Island was used to grow individuals of *M. assurgentiflora* that were then planted on East Anacapa Island (Sarah Chaney, personal communication).

Malva assurgentiflora subsp. *glabra* is known from four naturally occurring populations on San Clemente Island and two naturally occurring populations on Santa Catalina Island. San Clemente Island, owned and operated by the US Navy, has a restoration program targeting subsp. *glabra*. Seed from the small, naturally occurring populations has been used to grow a large number of plants that have been installed in several new populations on the island (Julie Lambert, personal communication). This restoration program has been successful, demonstrating that aggressive restoration activities can bring the taxon back from the brink of extirpation, at least locally. On Santa Catalina Island, two naturally occurring populations grow on small, off-shore islets on the channel (north) side of the island: Bird Rock and Indian Rock. Although the Bird Rock population of between 100 and 150 individuals may be stable, protected within a large patch of cactus, this low elevation station is vulnerable to stochastic events, a risk that will only increase with rising sea levels due to climate change. The population on Indian Rock appears to be declining, with only five or so plants observed from the water in 2016 (Guilliams, personal observation). The Catalina Island Conservancy has created a number of populations across Catalina Island using seeds gathered from both of these populations.

The situation described above warrants continued or even increased action on the part of the land owners/managers on the Channel Islands and their conservation partners. With the removal of introduced ungulates across most of the Channel Islands (McEachern et al. 2016), on-the-ground restoration may be the best hope for the survival of these species on the Channel Islands, especially when augmented by conservation seed banking (Cohen et al. 1991; Maunder et al. 2004) and *ex-situ*

plantings in botanic gardens (Fant et al., 2016) as long-term insurance. The current focus on island mallows and other rare plants across the California Islands on the part of island owner/managers and other partners is encouraging. The current momentum should increasingly shift the Channel Islands rare plant narrative from "species on the edge of extinction" to "back from the brink".

Representative specimens (arranged by collection locality, from NW to SE; **indicates type material).

Malva assurgentiflora subsp. **assurgentiflora. USA. California.** San Miguel Island: *Blakley 4238*; *Philbrick B66-131*; *Philbrick B66-132*; *Philbrick B66-133*; *Philbrick, Greaves, & Junak B78-376*; *Greaves s.n.,* 29 Jun 1978; *Junak 5974*; *Smith 6913*. Santa Rosa Island: *Daily SR240, Dunkle 8529*; *Junak SR-210*; *Philbrick & Haller B65-221*; *Philbrick B65-222*; *Smith 10386*; *Turner s.n.,* 25 Oct 1952. Santa Cruz Island: *Hochberg 716*; *Junak SC-1074*; *Junak SC-1565*; *Junak SC-1847*. Anacapa Island: *Hoffmann, s.n.*, 22 Sep 1930; *Junak & Amick MA-36*; *Junak MA-197*; *Junak & Halvorson MA-221*; *Junak MA-247*; *Timbrook & Philbrick 652***; *Timbrook & Philbrick 653*. San Nicolas Island: *Daily 86*; *Daily SNI94*; *Garoutte & Knapp CSG-2*; *Garoutte & Knapp CSG-3*; *Garoutte & Knapp CSG-4*; *Garoutte & Knapp CSG-5; Garoutte & Knapp CSG-6*; *Garoutte & Knapp CSG-7*; *Garoutte & Knapp CSG-8*; *Garoutte & Knapp CSG-9*; *Garoutte & Knapp CSG-10*; *Garoutte & Knapp CSG-11*; *Guilliams 2801*; *Junak SN-422*; *Junak SN-424*; *Junak SN-842*; *Junak SN-1041*; *Junak SN-1288*; *Junak SN1290*; *Junak SN-1291*; *Junak SN-1292*; *Newman 116*; *Vanderwier s.n.,* 6 Mar 1985. San Clemente Island: *Simpson 2212*. Santa Catalina Island: *Blakley 5395*; *Philbrick & Thorne B67-322*; *Ratay & Davis 131*; *Guilliams 3368*. California Mainland: *Benedict s.n.*, 17 Nov 1967; *Benedict s.n.*, 2 Mar 1969; *Bornstein s.n.*, 1 Mar 1992; *Burgess & Munro 4200*; *Dearing 2299*; *Halvorson 84-01*; *Hoffmann s.n.*, 15 Sep 1927; *Junak s.n.*, 7 Mar 1978; *Junak s.n.*, 9 Apr 1978; *Kuizenga s.n.*, 15 Jul 1979; *Kuizenga s.n.*, 1 Mar 1980; *Kuizenga s.n.*, 26 Jun 1987; *Murphey s.n.*, 3 Dec 1981; *Pollard s.n.*, 6 Oct 1945; *Pollard s.n.*, 19 Oct 1962; *Pollard s.n.*, 10 Jul 1964; *Pollard s.n.,* 21 Dec 1967; *Pollard s.n.*, 10 Nov 1971; *Pollard s.n.*, 11 Feb 1972; *Rose 69093*; *Secrest s.n.*, 28 Nov 1948; *Smith 2580*; *Twisselmann 9195*; *Yates s.n.*, Sep 1895. **MÉXICO.** Todos Santos Island: *Guilliams 2902*; *Philbrick & Benedict B65-1554*; *Philbrick & Benedict B68-502*.

Malva assurgentiflora subsp. **glabra. USA. California.** Santa Catalina Island: *Blakley 4739***; *Blakley 5415*; *Daily SCat-7*; *Dunkle 1858*; *Fosberg 7167*; *Guilliams 3279*; *Guilliams 3280*; *Guilliams 3281*; *Guilliams 3282*; *Guilliams 3283*; *Guilliams 3284*; *Guilliams 3285*; *Guilliams 3286*; *Guilliams 3287*; *Guilliams 3288*; *Guilliams 3289*; *Guilliams 3290*; *Guilliams 3291*; *Guilliams 3292*; *Guilliams 3293*; *Guilliams 3294*; *Guilliams 3295*; *Guilliams 3296*; *Guilliams 3297*; *Guilliams 3298*; *Guilliams 3310*; *Hoefs and Phelps 2282*; *Moran 625*; *Thorne 35794*. San Clemente Island: *Beauchamp & Douglas 3208*; *Beauchamp 4152*; *Benedict s.n.*, 27 Jun 1971; *Blakley 6414*; *Boutin 1623*; *Junak, Hochberg, Ferguson SCl-9*; *Guilliams 2710*; *Guilliams 2711*; *Guilliams 2712*; *Guilliams 2715*; *Guilliams 2716*; *Guilliams 2719*; *Guilliams 2720*; *Guilliams & Lambert 2729*; *Junak SCl-277*; *Junak & Stubler SCl-620*; *Raven 17303*; *Raven 17579*; *Ross 5437*.

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FIRST REPORT OF *YOUNGIA JAPONICA* (ASTERACEAE) SPONTANEOUS IN NEW YORK

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ABSTRACT

Youngia japonica is spontaneous in four counties in New York, the first report of the species for the state. The species is documented with herbarium specimens preserved in NY and photographs in the global community science program, iNaturalist.

Youngia japonica (L.) DC. is a scapose, rosette forming annual herb in the Cichorieae tribe of the Asteraceae. It is a pantropical weed spreading rapidly in North America (USDA, NRCS 2019; Spurr 2006; Weakly 2015). New York and Pennsylvania are indicated for the range of *Youngia japonica* in the Flora of North America (Spurr 2006) and the USDA PLANTS database (USDA NRCS 2019), but the species is not reported in the Plants of Pennsylvania (Rhoades & Block 2007) or the Catalogue of the Vascular Plants of New York State or the New York Flora Atlas (Weldy et al. 2019; Werier 2017). No specimens from New York are known besides those cited here. *Youngia thunbergiana* DC. has been treated as a subspecies of *Y. japonica* (*Y. japonica* subsp. *elstonii* (Hochr.) Babc. & Stebbins.) and is also found in North America but differs in having leafy scapes (Urbatsch et al. 2013).

Voucher specimens. **New York.** New York Co.: New York City, Central Park, between 90th and 91st Streets and between 7th and 8th Avenues, W of the West Drive, on slope E of Safari Playground. 40.788098, -73.966561 (WGS84, ±25 m), ca 36 m elev., 7 Oct 2019, *Atha & Candiani 16078* (BH, MU, NY).

Figure 1. *Youngia japonica*. A. Basal rosette and base of naked scape. B. Capitulescence. Photographed and collected in Central Park, New York Co., New York, 7 October 2019, *Atha & Candiani 16078* (BH).

Figure 1. *Youngia japonica* collected in Central Park, New York Co., New York, 7 October 2019, *Atha and Candiani 16078* (NY).

Several *Youngia japonica* plants were observed at the collection site in Central Park. They were growing in a bed densely planted with *Euonymus fortunei* obtained from a nursery in Lancaster, Pennsylvania. *Youngia japonica* has also been observed in New York, Kings, Queens, and Ulster counties, New York (iNaturalist 2019). Outside its native range, the species usually occurs in gardens, lawns, roadsides and other disturbed areas but is reported to be spreading into natural areas (Weakley 2015).

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DROSERA BREVIFOLIA (DROSERACEAE), NEW TO THE FLORA OF MARYLAND

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ABSTRACT

Drosera brevifolia is reported here as a new addition to the flora of Maryland and a northern range extension from southeast Virginia.

The diminutive *Drosera brevifolia* Pursh (dwarf sundew, red sundew) was previously known on the Atlantic Coastal Plain from southern Florida to southeastern Virginia (Weakley 2015) — it is now known to occur further north on the Eastern Shore of Maryland in Worcester County. I discovered the Maryland population of *D. brevifolia* in 2016 and the site was revisited in 2019 by a group of interested botanists, who collected the voucher.

The population consists of small, scattered colonies on bare, poorly drained sandy/peaty soil in open areas of a Nature Conservancy-owned site that was formerly an industrial pine plantation. The site has been clear-cut to restore and improve habitat conditions and it experiences periodic mowing and controlled fires. Several other state-rare plants occur at this site and *D. intermedia* is a common associate of the *D. brevifolia* colonies. The core of the *D. brevifolia* population is within the restoration site, but several plants were found along an adjacent roadside with the same soil and moisture conditions. One hundred to 200 individuals are currently estimated to occur here.

Voucher. **Maryland.** Worcester Co.: Nature Conservancy Nassawango Preserve habitat restoration site (details withheld because of rare plants at the site), clear-cut in the past, dwarf sundews rare overall but frequent in scattered patches on moist bare ground in full sun, acidic/sandy/peaty soil, with *Drosera intermedia*, 8 May 2019, *McAvoy 7843 with J. Harrison, C. Howard and R. Wilson* (DOV).

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NEW COMBINATIONS, NEW NAMES, TYPIFICATIONS, AND A NEW SECTION, SECT. *HISPANICA*, IN *KOELERIA* (POEAE, POACEAE)

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ABSTRACT

Based on morphological and molecular evidence we transfer the species of *Trisetum* sect. *Trisetaera, T. hispidum,* and *Trisetokoeleria taymirica* into *Koeleria*, describe *Koeleria* sect. *Hispanica*, and provide a new generic emendation. A total of 49 new combinations or new names are included. Additionally, we lectotypify *Avena clarkei* Hook f., *Avena micans* Hook. f., *Avena subalpestris* Hartm., *Avena subspicata* var. *agrostidea* Laest., *Trisetum pubiflorum* Hack., *Trisetum spicatum* f. *minor* Kom., and *Trisetum spicatum* f. *umbrosum* Kom.

RESUMEN

De acuerdo con diversas pruebas de carácter morfológico y molecular, transferimos las especies de *Trisetum* sect. *Trisetaera, T. hispidum* y *Trisetokoeleria taymirica* a *Koeleria*, describimos *Koeleria* sect. *Hispanica* y enmendamos la descripción de este género. Presentamos un total de 49 combinaciones o nombres nuevos. Además, designamos lectotipos para *Avena clarkei* Hook f., *Avena micans* Hook. f., *Avena subalpestris* Hartm., *Avena subspicata* var. *agrostidea* Laest., *Trisetum pubiflorum* Hack., *Trisetum spicatum* f. *minor* Kom. y *Trisetum spicatum* f. *umbrosum* Kom.

Recently there has been considerable progress in the systematics of *Trisetum* Pers. [Poeae: Pooideae: Poaceae; type *T. flavescens* (L.) P. Beauv.], a group of perennials with a complicated taxonomic history due to the variability and overlapping morphologies of its species and infrageneric taxa (Randall & Hilu 1986; Finot 2010). Recent molecular phylogenetic studies indicate that *Trisetum* is polyphyletic (Soreng & Davis 2000; Quintanar et al. 2007; Saarela et al. 2017; Barberá et al. 2019; Peterson et al. 2019) and now includes only two or three species. Another interesting aspect

in the systematics of *Trisetum* is the corroboration of these phylogenetic studies of the close relationship of *Trisetum* sect. *Trisetaera* Asch. & Graebn. [type *T. spicatum* (L.) K. Richt.] and species of *Koeleria* Pers. [type *K. pyramidata* (Lam.) P. Beauv.], also composed of perennials (cf. Saarela et al. 2017; Wölk & Röser 2017; Barberá et al. unpublished). Species of *T.* sect. *Trisetaera* and *Koeleria* usually share a similar inflorescence architecture with compact, dense, ovate-spiciform panicles. Both groups are meso- to xerophytic grasses distributed throughout the temperate regions of the Holarctic and Antarctic floristic kingdoms, occurring at medium to high altitudes in the Paleotropical, Neotropical, and Cape kingdoms (Clayton & Renvoize 1986; Watson & Dallwitz 1992; Quintanar et al. 2010). These grasses live in open places from sea level to high montane forests and are found mainly in xeric grassland communities, frequently on rocky soils (Tutin et al. 1980; Tzvelev 1976; Clayton & Renvoize 1986).

Trisetum sensu stricto is characterized in having more or less open, loose panicles, unequal glumes, clearly bifid lemmas apices with a bent or slightly bent dorsal awn more or less twisted at the base that is inserted in the upper third (Barberá et al. 2018). *Trisetum* sect. *Trisetaera* is morphologically distinguished in having narrow panicles with densely clustered spikelets arranged on short, hairy branches, usually comparatively larger and sometimes subequal glumes, bidentate lemmas with a dorsal awn also inserted in the upper third, normaly at a more distal position than in *Trisetum*, usually the awn basally to sub-basally bent, but not twisted. Reichenbach (1830) was the first to recognize the similarities between *Koeleria* and *Trisetum* by making a combination in *Koeleria* [*K. subspicata* (L.) Rchb., nom. illeg. superfl. = *Trisetum spicatum*]. Tzvelev (2011) pointed out that *T.* sect. *Trisetaera* was morphologically very similar to *Koeleria*. The species of *Koeleria* usually have dense and spike-like panicles, relatively large and sometime subequal glumes but the lemmas are muticous, mucronate or, much more rarely, apically or subapically short-awned (Quintanar & Castroviejo 2013). In addition to these characters, the species of *T.* sect. *Trisetaera* do not have conspicuous and marked apical lateral awns but have two short awnlets which are sometime missing (Hultén 1959; Tzvelev 1976, 2011), also seen in *Koeleria*. In a revision of *Trisetum* for northern Asia, *T.* subsect. *Koeleriformia* Enushch. was erected to indicate similarities with *Koeleria* (Enushchenko 2011).

Based on a large unpublished molecular DNA sequence study using four gene regions (ITS, *rpl32-trnL* spacer, *rps16-trnK* spacer, and *rps16* intron), we proposed to move the *T. spicatum* complex into *Koeleria* (Soreng et al. 2017). This was supported by Saarela et al. (2017), who included many representatives of *T.* sect. *Trisetaera, Koeleria,* and other taxa considered to belong to the subtribe Koeleriinae Asch. & Graebn. Our current study includes a more extensive sampling of these groups allowing a deep exploration of the relationships between *T.* sect. *Trisetaera* and *Koeleria,* and we now feel confident in making taxonomic changes that were previously tentatively proposed. Nested in our *Koeleria* clade, we find the Scandinavian and Northern Asian *T. subalpestre* (Hartm.) Neuman, the Iberian endemic *T. hispidum* Lange, and the Asiatic hybrid × *Trisetokoeleria taymirica* Tzvelev. *Trisetum subalpestre*, included by Enuschenko (2011) in *T.* sect. *Trisetaera* subsect. *Agrostidea* Prob., is morphologically similar to species included in *T.* sect. *Trisetaera* in having loosely caespitose culms with a spiciform, densely flowered panicle, and lemmas with a dorsal awn inserted in the upper third (Jonsell 1980). *Trisetum hispidum*, previously classified in the heterogeneous *T.* sect. *Hispanica* Chrtek, shares with *T.* sect. *Trisetaera* and *Koeleria* its densely-flowered, compact panicles and relatively large glumes, and its appearance at first glance resembles a robust species of *Koeleria*.

Based on our unpublished molecular DNA phylogeny, we transfer the species of *Trisetum* sect. *Trisetaera, T. hispidum,* and *Trisetokoeleria taymirica* into *Koeleria*, describe *Koeleria* sect. *Hispanica,* and emend the generic description. A total of 49 new combinations or new names are

made. In addition, lectotypes are chosen for seven names. We now recognize *Koeleria* in a broad sense as a single, albeit larger, natural genus.

MATERIAL AND METHODS

Taxonomic arrangements are based on our current on-going molecular DNA sequence studies. We have examinated herbarium specimens using the following taxonomic treatments (Domin 1907; Tzvelev 1976, 2011; Tutin et al. 1980; Randall & Hilu 1986; Edgar 1998; Edgar & Gibb 1999; Finot et al. 2004, 2005a, 2005b; Finot 2010; Quintanar & Castroviejo 2013). Taxa that we lack molecular evidence for are preceded by an asterisk (*). The new combinations and new names are listed in **bold** letters. Lectotypifications were made after a thorough review of the material cited in the protologue and study of herbarium vouchers. In addition, we provide a list of unplaced names where we lack adequate information to assess their systematic placement.

TAXONOMY

KOELERIA Pers., Syn. Pl. 1: 97. 1805, **gen. emend.** LECTOTYPE SPECIES: *Poa nitida* Lam. [=*Koeleria pyramidata* (Lam.) P. Beauv. subsp. *pyramidata*], designated by Nash in Britton & Brown 245. 1913.

Description—Perennials, erect and tufted, densely to loosely caespitose with intravaginal branches, also extravaginal in some species, sometimes short rhizomatous, the rhizomes 0.2–1.2(–82) mm long. Shoots with (1–)2–4(–7) leaves. Culms (4.5–)15–80(–100) cm tall, (0.18–)0.6–1(–2.2) mm wide, glabrous or hairy to villous below the panicle, erect to somewhat geniculate at the base. Leaves simple and alternate; leaf sheaths membranous, more or less firmly attached to the culm, open to the base; leaf blades (1.1–)2.9–6.5(–36) cm × (1–)3–5(–5.3) mm, linear, flat to folded, margins strongly involute, glabrous to minutely prickle-toothed or hairy. Ligules truncate, erose, sometime ciliolate. Inflorescences (0.7–)3.4–12(–15.4) cm long, paniculate, terminal, more or less compact with the spikelets densely clustered, spike-like to ovoid in outline, with entire and non-interrupted outlines to irregularly interrupted ones, the rachis not obvious or visible, hairy. Spikelets (2.2–)3.2–9(–10) mm long, laterally compressed, short-pedicellate with (1–)2–3(–5) hermaphrodite florets arranged on a rachilla, often prolonged beyond the uppermost floret and bearing an underdeveloped floret; disarticulation above the glumes and between the florets; callus very short, oblique, usually short-hairy, the hairs 0.02–1(–4) mm long. Glumes herbaceous, heteromorphic, unequal to almost equal in length, dissimilar in shape or more rarely similar; lower glumes (0.7–)2.3–6(–9.5) × (0.2–)0.5–1.5(–2.2) mm, 1(3)-veined, narrowly lanceolate, usually slightly shorter than the proximal lemma; upper glumes (1.7–)4.3–7(–9) × (0.4–)0.8–2.2(–2.8) mm, 3(5)-veined, slightly shorter or equal to or sometimes longer than the proximal lemma, broadly elliptic-lanceolate with hyaline margins, pointed, carinate, often short-mucronate, usually glabrous, very rarely hairy. Lemmas (1.9–)3–7.5(–9) × (0.3–)0.7–1.7(–2.6) mm, herbaceous, elliptic-lanceolate, strongly carinate, with hyaline margins, 3–5-veined, glabrous, papillose to minutely prickle-toothed; apex entire, pointed or bicuspid or bidentate, the teeth 0.2–0.3(–0.9) mm long, blunt or bearing two lateral awnlets (0.3)0.7–1.1(–1.7) mm long, sometimes just mucronate, with mucro 0.1–0.2(–1) mm long, apically to subapically attached, or with a dorsal awn (2–)2.5–6.5(–11.5) mm, usually basally to subbasaly bent and not twisted, inserted 0.7–2.1(–2.4) mm from the lemma apex, at its upper quarter, often almost subapical. Paleas (2–)2.2–5.6(–8) mm long, hyaline, gaping during anthesis, apically notched to bifid, 2-veined and 2-keeled, minutely prickle-toothed. Stamens 3, with anthers (0.3–)0.8–2(–2.5) × (0.1–)0.2–0.3(–1.2) mm. Ovary glabrous, bearing 2 feathery stigmas on short free styles. Lodicules 2, (0.2–)0.6–1.3(–1.5) mm long, hyaline, one-to-several times toothed, frequently 2-toothed or obscurely toothed. Caryopsis (1.6–)2.1–2.7(–3.8) mm long, slightly laterally compressed, the hilum short, punctiform; endosperm soft-liquid (containing lipids) in the mature fruit. Basic chromosome number $x = 7$.

Comments—Overall the approximate number of species in the genus increases from 53 (Quintanar et al. 2010) to 79.

KOELERIA section **TRISETAERA** (Asch. & Graebn.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum* sect. *Trisetaera* Asch. & Graebn., Syn. Mitteleur. Fl. 2: 270. 1899. *Trisetum* subsect. *Koeleriformia* Enushch., Novosti Sist. Vyssh. Rast. 42 (5): 60. 2011, nom. illeg. hom., non Louis-Marie. **TYPE**: *Aira spicata* L. [≡ *Koeleria spicata* (L.) Barberá, Quintanar, Soreng, & P.M. Peterson].

= *Trisetokoeleria* Tzvelev, Novosti Sist. Vyssh. Rast. 7: 73. 1971, pro hybrid. **TYPE**: *Koeleria gorodkowii* Roshev.

= *Trisetum* (sect. *Trisetaera*) subsect. *Agrostidea* Prob., Novosti Sist. Vyssh. Rast. 15: 20. 1979. **TYPE**: *T. agrostideum* (Laest.) Fr. (= *Avena subalpestris* Hartm.).

Koeleria antarctica (G. Forst.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Aira antarctica* G. Forst., Fl. Ins. Austr. 8, no. 41. 1786. *Danthonia antarctica* (G. Forst.) Spreng., Syst. Veg. ed. 16, 1: 331. 1824. *Trisetum antarcticum* (G. Forst.) Trin., Mém. Acad. Imp. Sci. St.-Pétersbourg, sér. 6, Sci. Math. 1 (1): 61. 1830.

***Koeleria arduana** (Edgar & A.P. Druce) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum arduanum* Edgar & A.P. Druce, New Zealand J. Bot. 36: 545, fig. 3. 1998.

Koeleria barbinodis (Trin.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum barbinode* Trin., Linnaea 10 (3): 300. 1836.

Koeleria barbinodis var. **sclerophylla** (Hack.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum sclerophyllum* Hack., Anales Mus. Nac. Buenos Aires 21: 108. 1911. *Trisetum barbinode* var. *sclerophyllum* (Hack.) Finot, Ann. Missouri Bot. Gard. 92 (4): 546. 2005.

***Koeleria barrosii** Barberá, Quintanar, Soreng, & P.M. Peterson, **nom. nov.** Replaced name: *Trisetum pyramidatum* Louis-Marie ex Finot, Ann. Missouri Bot. Gard. 92 (4): 558, fig. 3. 2005. **TYPE**: Chile. Punta Arenas, Leña Dura, 28 Jan 1946, *E. Barros 5706* (holotype: US-1869901!).

Comments—The new name honors Ernesto Barros (1887–1954), a Chilean collector. Finot et al. (2005a) mistakenly gave credit to Manuel Barros (1880–1973) for collecting the type. However, the holotype specimen at US clearly attributes the collection to E. Barros.

Koeleria drucei (Edgar) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum drucei* Edgar, New Zealand J. Bot. 36: 548, fig. 5. 1998.

Koeleria hookeri Barberá, Quintanar, Soreng, & P.M. Peterson, **nom. nov.** Replaced name: *Avena clarkei* Hook f., Fl. Brit. India 7 (22): 278. 1896. *Trisetum clarkei* (Hook. f.) R.R. Stewart, Brittonia 5 (4): 431. 1945. **LECTOTYPE** (**designated here**): **India**. Kashmir, Budrawur [Bhadarwāh], 32°58'N 75°43'E, *C.B. Clarke 31514* (K-32261!).

Comments—Recommendation 23A.2 of the International Code of Nomenclature (Turland et al. 2018) recommends avoidance of the use of the genitive and the adjectival form of the same word to designate two different species of the same genus. Because there is a name at specific rank, *Koeleria clarkeana* Domin, Biblioth. Bot. 14 (65): 272, pl. 18 fig. 11. 1907, currently treated as a species of *Rostraria* Trin., we have decided to avoid the name that would result from combining the

basionym of this species and to provide a new name that honors Joseph Dalton Hooker (1817–1911), who described this species for the first time.

Koeleria inaequalis (Whitney) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum inaequale* Whitney, Occas. Pap. Bernice Pauahi Bishop Mus. 13: 171. 1937.

***Koeleria johnstonii** (Louis-Maire) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum oreophilum* var. *johnstonii* Louis-Maire, Rhodora 30 (360): 237. 1929. *Trisetum johnstonii* (Louis-Marie) Finot, Curr. Topics Pl. Sci. 11: 60. 2010.

Koeleria johnstonii subsp. **mattheii** (Finot) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum mattheii* Finot, Ann. Missouri Bot. Gard. 92 (4): 551, fig. 1. 2005. *Trisetum johnstonii* subsp. *mattheii* (Finot) Finot, Curr. Topics Pl. Sci. 11: 60. 2010.

***Koeleria kangdingensis** (Z.L. Wu) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum clarkei* var. *kangdingense* Z.L. Wu, Acta Biol. Plateau Sin. 2: 16. 1984. *Trisetum kangdingense* (Z.L. Wu) S.M. Phillips & Z.L. Wu, Fl. China 22: 326. 2006.

***Koeleria koidzumiana** (Ohwi) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum koidzumianum* Ohwi, Acta Phytotax. Geobot. 2: 33. 1933.

***Koeleria lasiorhachis** (Hack.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum antarcticum* var. *lasiorhachis* Hack., Man. New Zealand Fl.: 880. 1906. *Trisetum lasiorhachis* (Hack.) Edgar, New Zealand J. Bot. 36: 549, fig. 7. 1998.

***Koeleria lepida** (Edgar & A.P. Druce) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum lepidum* Edgar & A.P. Druce, New Zealand J. Bot. 36: 553, fig. 9. 1998.

Koeleria ligulata (Finot & Zuloaga) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum ligulatum* Finot & Zuloaga, Ann. Missouri Bot. Gard. 91(1): 15, fig. 1. 2004.

***Koeleria micans** (Hook. f.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Avena micans* Hook. f., Fl. Brit. India 7: 279. 1896. *Trisetum micans* (Hook. f.) Bor, Grass. Burma, Ceylon, India & Pakistan: 448. 1960. **LECTOTYPE (designated here)**: **India**. Uttarakhand state, Garhwal division, Tehri Garhwal, 30º30'N 78º30'E, *J.F. Duthie 46* (K-000032268!).

***Koeleria nancaguensis** (Finot) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum nancaguense* Finot, Ann. Missouri Bot. Gard. 92 (4): 553, fig. 2. 2005.

Koeleria oreophila (Louis-Maire) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum oreophilum* Louis-Maire, Rhodora 30 (359): 221. 1928.

Koeleria oreophila subsp. **barbatipalea** (Hultén ex Veldkamp) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* var. *barbatipaleum* Hultén ex Veldkamp, Gard. Bull. Singapore 36 (1): 135. 1983. *Trisetum barbatipaleum* (Hultén ex Veldkamp) Finot, Contr. U.S. Natl. Herb. 48: 661. 2003. *Trisetum oreophilum* subsp. *barbatipaleum* (Hultén ex Veldkamp) Finot, Curr. Topics Pl. Biol. 11: 62. 2010.

Koeleria oreophila subsp. **colombiana** (Finot) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum oreophilum* subsp. *colombianum* Finot, Curr. Topics Pl. Sci. 11: 60. 2010.

Koeleria oreophila subsp. **rosei** (Scribn. & Merr.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum rosei* Scribn. & Merr., Contr. U.S. Natl. Herb. 8 (4): 289. 1905. *Trisetum oreophilum* subsp. *rosei* (Scribn. & Merr.) Finot, Curr. Topics Pl. Biol. 11: 63. 2010.

Koeleria preslii (Kunth) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Avena preslii* Kunth, Enum. Pl. 1: 304. 1833 ["Preslei"]. *Avena pilosa* J. Presl, Reliq. Haenk. 1 (4–5): 253. 1830, nom. illeg. hom. *Trisetum preslii* (Kunth) É. Desv., Fl. Chil. 6: 347. 1854.

Koeleria projecta (Louis-Marie) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum projectum* Louis-Marie, Rhodora 30 (359): 217. 1928. *Trisetum cernuum* var. *projectum* (Louis-Marie) Beetle, Leafl. W. Bot. 4 (12): 288. 1946. *Trisetum spicatum* var. *projectum* (Louis-Marie) J.T. Howell, Wasmann J. Biol. 37 (12): 22. 1979.

***Koeleria serpentina** (Edgar & A.P. Druce) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum serpentinum* Edgar & A.P. Druce, New Zealand J. Bot. 36: 554, fig. 11. 1998.

Koeleria spicata (L.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** non Reichb. ex Willk. & Lange, Prodr. Fl. Hispan. 1: 72. 1861, nom. inval. Basionym: *Aira spicata* L., Sp. Pl.: 64. 1753. *Avena subspicata* Clairv., Man. Hebor. Suisse: 17. 1811. *Trisetum spicatum* (L.) K. Richt., Pl. Eur. 1: 59. 1890. *Trisetaria spicata* (L.) Paunero, Anales Jard. Bot. Madrid 9: 516. 1950. **Figure 1A–E**.

= *Trisetum pubiflorum* Hack., Oesterr. Bot. Z. 52: 187. 1902. *Trisetum spicatum* var. *pubiflorum* (Hack.) L. Liou, Vasc. Pl. Hengduan Mount. 2: 2224. 1994. **LECTOTYPE** (**designated here**): **China**. Kashmir, Shaksgam Valley, 36°09'N 76°37'E, 12 Aug 1893, *J.F. Duthie 13543* (W-1916-0031902!; isolectotypes: K images!, US-868575!, US-101514 fragment!).

= *Trisetum spicatum* f. *minor* Kom., Fl. Kamtschatka 1: 156. 1927. **LECTOTYPE** (**designated here**): **Russia**. Kamchatka Peninsula, outside Krasheninnikov crater, 54°35'N 160°16'E, 19 Aug 1909, *V. Komarov 3243* (LE!).

= *Trisetum spicatum* f. *umbrosum* Kom., Fl. Kamtschatka 1: 156. 1927. **TYPE**: **Russia**. Kamchatka Peninsula, near Ganal, 53°41'N 157°37'E, 13 Jul 1909, *V. Komarov 2725* (lectotype, **designated here**: LE!; isolectotype: LE!).

Koeleria spicata subsp. **andina** (Benth.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum andinum* Benth., Pl. Hartw.: 261. 1847. *Trisetum spicatum* var. *andinum* (Benth.) Louis-Marie, Rhodora 30 (360): 239. 1929. *Trisetum spicatum* subsp. *andinum* (Benth.) Hultén, Svensk Bot. Tidskr. 53 (2): 224. 1959.

Koeleria spicata subsp. **alaskana** (Nash) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum alaskanum* Nash, Bull. New York Bot. Gard. 2: 155. 1901. *Trisetum spicatum* var. *alaskanum* (Nash) Louis-Marie, Rhodora 30: 239. 1928. *Trisetum spicatum* subsp. *alaskanum* (Nash) Hultén, Svensk Bot. Tidskr. 53: 210. 1959. *Trisetum molle* subsp. *alaskanum* (Nash) Rebr., Arktic. Fl. SSSR 2: 100. 1964.

***Koeleria spicata** subsp. **australiensis** (Hultén ex Veldkamp) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *australiense* Hultén ex Veldkamp, Gard. Bull. Singapore 36 (1): 135. 1983.

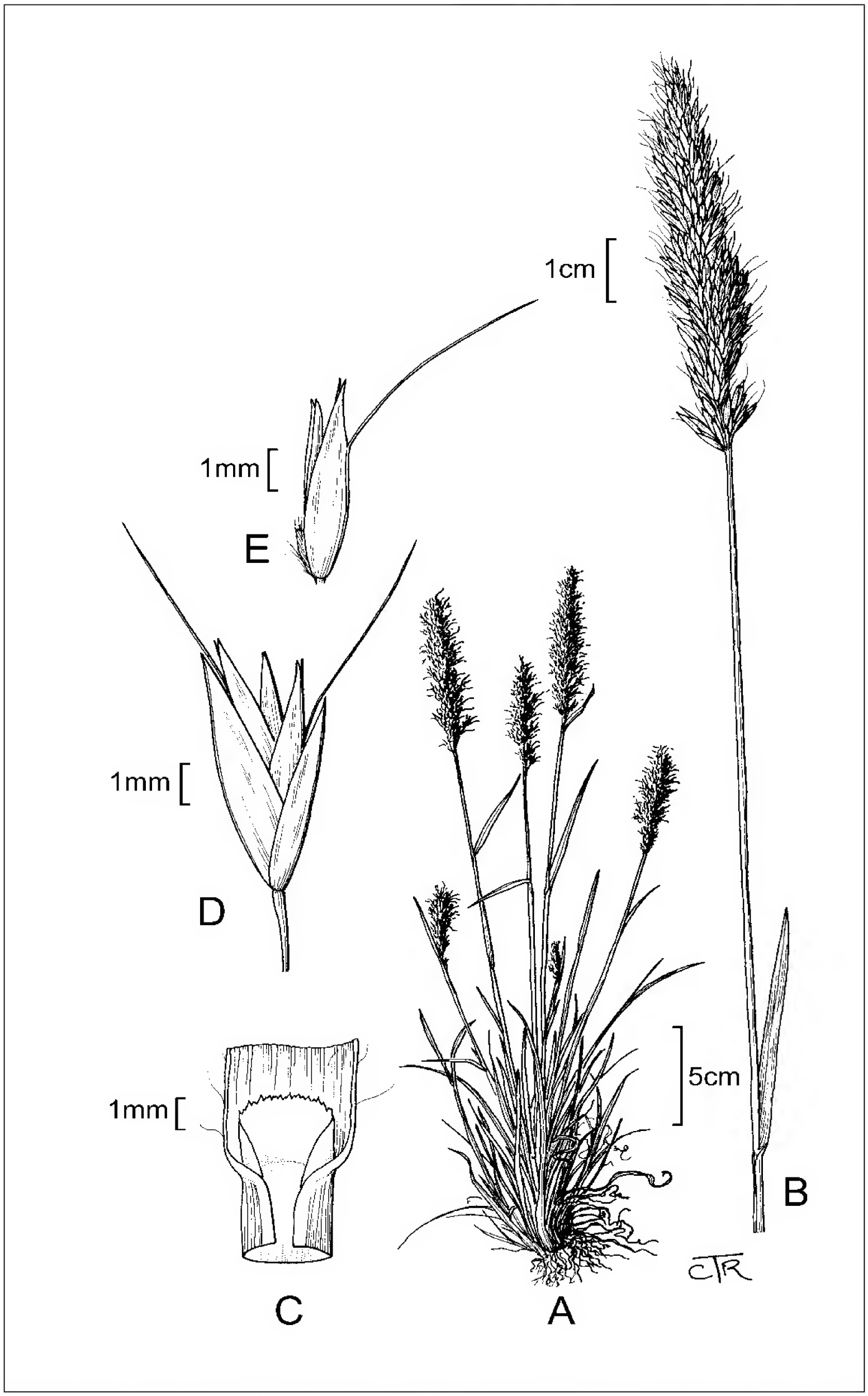

Figure 1. *Koeleria spicata*. A. Habit. B. Culm. C. Ligule. D. Spikelet. E. Floret. Drawn by Cindy T. Roche for the Flora of North America.

Koeleria spicata subsp. **cumingii** (Nees) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Koeleria cumingii* Nees, Syn. Pl. Glumac. 1: 294. 1854. *Trisetum cumingii* (Nees) Nicora, Fl. Patagónica 3: 250. 1978. *Trisetum spicatum* var. *cumingii* (Nees) Finot, Ann. Missouri Bot. Gard. 92 (4): 562–563. 2005. *Trisetum spicatum* subsp. *cumingii* (Nees) Finot, Finot, Curr. Topics Pl. Biol. 11: 67. 2010.

***Koeleria spicata** subsp. **dianthema** (Louis-Marie) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* var. *dianthemum* Louis-Marie, Rhodora 30 (360): 239. 1929. *Trisetum biflorum* Phil., Anales Univ. Chile 48: 568. 1873, nom. illeg. hom. *Trisetum dianthemum* (Louis-Marie) Finot, Contr. U.S. Natl. Herb. 48: 664. 2003. *Trisetum spicatum* subsp. *dianthemum* (Louis-Marie) Finot, Curr. Topics Pl. Biol. 11: 66. 2010.

***Koeleria spicata** subsp. **geghamensis** (Gabrieljan) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum geghamense* Gabrieljan, Fl. Rastitel'nost' Rastitel'nye Resursy Armyansk. S.S.R. 16: 11-12. 2007.

***Koeleria spicata** subsp. **himalaica** (Hultén ex Veldkamp) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *himalaicum* Hultén ex Veldkamp, Gard. Bull. Singapore 36 (1): 135. 1983.

***Koeleria spicata** subsp. **hultenii** (Chrtek) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *hultenii* Chrtek, Acta Univ. Carol., Biol. 1967: 101. 1968.

***Koeleria spicata** subsp. **kinabaluensis** (Chrtek) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *kinabaluense* Chrtek, Folia Geobot. Phytotax. 5: 447. 1970.

Koeleria spicata subsp. **mollis** (Kunth) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum molle* Kunth, Révis. Gramin. 1: 101. 1829. *Avena mollis* Michx., Fl. Bor.-Amer. 1: 72. 1803, nom. illeg. hom. *Trisetum spicatum* var. *molle* (Kunth) Beal, Grass. N. Amer. 2: 377. 1896. *Trisetum triflorum* subsp. *molle* (Kunth) Á. Löve & D. Löve, Univ. Colorado Stud., Ser. Biol. 17: 7. 1965. *Trisetum spicatum* subsp. *molle* (Kunth) Piper, Contr. U.S. Natl. Herb. 11: 125. 1906.

***Koeleria spicata** subsp. **mongolica** (Hultén ex Veldkamp) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *mongolicum* Hultén ex Veldkamp, Gard. Bull. Singapore 36 (1): 135. 1983. *Trisetum mongolicum* (Hultén ex Veldkamp) Peshkova, Fl. Centr. Sibir. 1: 97. 1979.

Koeleria spicata subsp. **ovatipaniculata** (Vasey) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *ovatipaniculatum* Hultén ex Jonsell, Svensk Bot. Tidskr. 69 (2): 132. 1975. *Trisetum ovatipaniculatum* (Hultén ex Jonsell) Galushko, Novosti Sist. Vyssh. Rast. 13: 254. 1976. *Trisetaria spicata* subsp. *ovatipaniculata* (Hultén ex Jonsell) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135 (2): 385. 1996.

Koeleria spicata subsp. **phleoides** (d'Urv.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Avena phleoides* d'Urv., Fl. Iles Malouin. 30, 19. 1825. *Trisetum phleoides* (d'Urv.) Kunth, Révis. Gramin. 1: 101. 1829. *Trisetum subspicatum* var. *phleoides* (d'Urv.)

Hack., Svenska Exped. Magell. 3 (5): 222. 1900. *Trisetum spicatum* subsp. *phleoides* (d'Urv.) Macloskie, Rep. Princeton Univ. Exp. Patagonia, Botany 8 (1,5,1): 206. 1904.

***Koeleria spicata** subsp. **tibetica** (P.C. Kuo & Z.L. Wu) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum tibeticum* P.C. Kuo & Z.L. Wu, Fl. Xizang. 5: 188, pl. 93 figs. 1–3. 1987. *Trisetum spicatum* subsp. *tibeticum* (P.C. Kuo & Z.L. Wu) Dickoré, Stapfia 39: 201. 1995.

Koeleria spicata subsp. **virescens** (Regel) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Avena flavescens* var. *virescens* Regel, Bull. Soc. Imp. Naturalistes Moscou 41 (3–4): 299. 1868. *Trisetum fedtschenkoi* Henrard, Blumea 3 (3): 425. 1940. *Trisetum spicatum* subsp. *virescens* (Regel) Tzvelev, Novosti Sist. Vyssh. Rast. 7: 65. 1971. 1970.

Koeleria spicata subsp. **wrangelensis** (V.V. Petrovsky) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum spicatum* subsp. *wrangelense* V.V. Petrovsky, Bot. Zhurn. (Kiev) 63 (9): 1263. 1978. *Trisetum wrangelense* (V.V. Petrovsky) Prob., Sosud. Rast. Sovetsk. Dal'nego Vostoka 1: 163. 1985.

Koeleria subalpestris (Hartm.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Avena subalpestris* Hartm., Handb. Skand. Fl., ed. 3: 21. 1838. *Trisetum subalpestre* (Hartm.) Neuman, Sver. Fl.: 755. 1901. *Trisetaria subalpestris* (Hartm.) Banfi & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civico Storia Nat. Milano 135 (2): 385. 1996. **LECTOTYPE** (**designated here**): **Sweden**. Lapland, Norrbotten County, Karesuando, Maunu, 68°28'N 22°12'E, *L.L. Laestadius III.92* (UPS-V-077305!; isolectotypes: BM-001034617!, LE-10136!, MO-2106460!, P-2222191!, UPS-V-103570!, UPS-V-105878!, UPS-V-232821!).

= *Avena subspicata* var. *agrostidea* Laest., Nova Acta Regiae Soc. Sci. Upsal. 11: 245. 1839. *Trisetum agrostideum* (Laest.) Fr., Novit. Fl. Suec. Mant. 3 (12): 180. 1845. **LECTOTYPE** (**designated here**): **Sweden**. Norrbottens Län (not stated), Karesuando, 1837, *L.L. Laestadius s.n.* (W-24520!).

Koeleria taymirica (Tzvelev) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** *Trisetokoeleria taymirica* Tzvelev, Novosti Sist. Vyssh. Rast. 11: 72. 1974, pro hybrid.

Koeleria tenella (Petrie) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum antarcticum* subsp. *tenellum* Petrie, Trans. & Proc. New Zealand Inst. 44: 187. 1912. *Trisetum antarcticum* var. *tenellum* (Petrie) Cheeseman, Man. New Zealand Fl.: 169. 1925. *Trisetum tenellum* (Petrie) A.W. Hill, Index Kew. Suppl. 9: 289. 1938.

Koeleria vaseyi Barberá, Quintanar, Soreng, & P.M. Peterson, **nom. nov.** Replaced name: *Trisetum montanum* Vasey, Bull. Torrey Bot. Club 13 (7): 118. 1886. *Trisetum spicatum* subsp. *montanum* (Vasey) W.A. Weber, Phytologia 33 (2): 106. 1976.

Comments—The new name honors George Vasey (1822–1893), who first described this species.

Koeleria youngii (Hook. f.) Barberá, Quintanar, Soreng, & P.M. Peterson, **comb. nov.** Basionym: *Trisetum youngii* Hook. f., Handb. N. Zeal. Fl. 335. 1864.

Figure 2. *Koeleria hispanica* (≡ *Trisetum hispidum* lectotype) collected by *J. Lange* (C) in Spain.

KOELERIA section **HISPANICA** Barberá, Quintanar, Soreng, & P.M. Peterson, **sect. nov. TYPE**: *Trisetum hispidum* Lange.

Description—Culms hairy, the hairs 0.1–0.8 mm long. Leaves densely hairy, the hairs 0.1–1.3 mm long. Panicles subcylindric or ovate-lanceolate; rachis hairy. Lemmas 3-4 mm long, lanceolate, hairy, the hairs 0.2–0.6 mm long; apex bidentate, the teeth 0.2–0.6 mm long each bearing two lateral mucros 0.5–0.8 mm long, the dorsal or subapical awn 2.5–4 mm long inserted on upper quarter, the awn straight or bent near base. Anthers 1.8–2.5 mm long.

Koeleria hispanica Barberá, Quintanar, Soreng, & P.M. Peterson, **nom. nov.** Replaced name: *Trisetum hispidum* Lange, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1860: 42. 1861, non *Koeleria hispida* (Savi) DC. **TYPE**: **Spain**. [León Province, Villafranca del Bierzo] "In fissuris rupium ad Villafranca del Vierzo (prov. Legion.) reg. mont. inf.", 20 Jul 1851 or 1852, *J. M. Ch. Lange 61* (lectotype designated by Silva Pando & Pino Pérez, Bot. Complut. 43: 54. 2019: C-10017263 [image!]; isolectotype: C-1001264 [image!]). **Figure 2**.

Comments—The new name honors the territory (Hispania) where this species is endemic. This robust species of *Koeleria* has densely-flowered and lobate panicles, hairy 2–3-flowered spikelets with relatively large glumes. The lateral awnlets at the lemma apex are short but prominent and the dorsal awn is somewhat bent near its base and inserted on the upper quarter of the lemma. However, in our phylogenetic topologies it appears to be closer to *K.* sect. *Koeleria* than to representatives of *T.* sect. *Trisetaera*. We erect a monotypic section for this curious species that shows characters that do not fit in the existing sections of *Koeleria*.

Unplaced taxa

Trisetum ambiguum Rúgolo & Nicora, Bol. Soc. Argent. Bot. 25 (3–4): 468. 1988.
Trisetum longiglume Hack., Repert. Spec. Nov. Regni Veg. 7: 319. 1909.
Trisetum longiglume var. *glabratum* Nicora, Fl. Patag. 3: 245. 1978.
Trisetum macbridei Hitchc., Contr. U.S. Natl. Herb. 24 (8): 359. 1927.

Comments—The placement of *T. ambiguum*, *T. longiglume*, and *T. macbridei* in our molecular phylogeny is incongruent between our plastid and ITS topologies, i.e., they align in the different clades within the Koeleriinae, probably indicating a reticulate origin.

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FLORA OF NORTHERN ALABAMA, PART 4. BASAL MONOCOTS: ACORALES AND ALISMATALES SWEETFLAG TO PONDWEEDS

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ABSTRACT

This paper is a floristic guide to native and naturalized monocots in the orders Acorales and Alismatales found within the Interior Plains and Appalachian Highlands of northern Alabama. Families included in this treatment are: Acoraceae, Araceae, Alismataceae, Tofieldiaceae, Hydrocharitaceae, and Potamogetonaceae. Identification keys, photographs, maps of occurrence in northern Alabama, habitats, flowering and fruiting times, distributional data, pertinent synonymy, and comments are provided for each taxon.

Flowering plants (angiosperms) have historically been separated into two distinct groups, distinguished by characteristic differences such as leaf venation, organization of floral structures, and the number of cotyledons (embryonic seed leaves). Dicots or dicotyledons are plants having leaves with netted venation, tetramerous or pentamerous (four or five-parted) flowers, and two cotyledons. Monocots or monocotyledons are plants having parallel venation, grass-like leaves, trimerous (three-parted) flowers, and a single cotyledon. These two assemblages, once believed to represent natural groups have been recognized as Class Magnoliopsida (dicots) and Class Liliopsida (monocots) (Takhtajan 1980; Cronquist 1981).

Angiosperms clearly are monophyletic, but their traditional classification into monocots and dicots is not phylogenetically supported (Soltis et al. 2018). One problem associated with this binary classification is the existence of plants displaying a mixture of both dicot- and monocot-like features. Phylogenetic studies revealed that these “hard to classify, primitive dicots" are in reality a disparate assemblage of early-divergent species and that their unusual traits are plesiomorphic (primitive)

features that arose early in angiosperm evolution. Specifically, plants classified as dicots are not monophyletic but actually a paraphyletic grade from which monocots evolved (Soltis et al. 2018).

While dicots as traditionally recognized have been shown to be polyphyletic, recent phylogenetic studies utilizing both molecular and morphological data have found strong support for monophyly of the monocots (Soltis et al. 2018). Morphological synapomorphies (shared advanced traits) uniting the monocots include the presence of a single cotyledon, parallel-veined leaves, adventitious root systems, and scattered vascular bundles within the stem (Soltis et al. 2018). Despite agreement on the group's monophyly, phylogenetic studies differ in their placement of monocots relative to other major angiosperm clades; a comprehensive understanding of early angiosperm relationships is lacking (Soltis et al. 2018).

With a recent estimate of 74,273 species globally, monocots comprise approximately 25% of all flowering plants (Christenhusz & Byng 2016). Of the approximately 4,200 vascular plant species in Alabama, about 27% are monocots (Keener et al. 2019). The current paper treats 45 species of monocots (Fig. 1) within the orders Acorales (Acoraceae) and Alismatales, which include the following families: Alismataceae, Araceae, Hydrocharitaceae, Potamogetonaceae, and Tofieldiaceae (Table 1). The families treated in this paper are often referred to as basal monocots because the fossil record of Acorales and Alismatales extends back to the Cretaceous (Stockey 2006). Igersheim et al. (2001) states that "*Acorus* (Acoraceae) is the basalmost clade among extant monocots, followed by Araceae and Alismatales."

Table 1. Taxonomic classification of basal monocots used for the flora of north Alabama.

ORDER ACORALES	
Family Acoraceae	*Acorus* (1 species)
ORDER ALISMATALES	
Family Araceae	*Arisaema* (4 species) *Arum* (1 species) *Colocasia* (1 species) *Landoltia* (1 species) *Lemna* (3 species) *Orontium* (1 species) *Peltandra* (1 species) *Pistia* (1 species) *Spirodela* (1 species) *Wolffia* (2 species) *Wolffiella* (1 species)
Family Tofieldiaceae	*Triantha* (1 species)
Family Alismataceae	*Alisma* (1 species) *Echinodorus* (1 species) *Sagittaria* (6 species)
Family Hydrocharitaceae	*Egeria* (1 species) *Elodea* (1 species) *Hydrilla* (1 species) *Limnobium* (1 species) *Najas* (3 species) *Vallisneria* (1 species)
Family Potamogetonaceae	*Potamogeton* (9 species) *Stuckenia* (1 species) *Zannichellia* (1 species)

Numerous taxonomic systems are available for the classification of plants into orders and families. Early treatises relied almost entirely on morphological evidence to show relationships of the angiosperms, including the monocots. Two widely used works are Cronquist's *An integrated System of Classification of Flowering Plants* (1981), which divided the monocots (Class Liliopsida) into 19 orders and 65 families, and Takhtajan's *Diversity and Classification of Flowering Plants* (1997), which recognized 58 orders and 133 families. A discussion of the taxonomic concepts used here is detailed below, along with a comparison of alternative treatments of orders and families.

With the benefit of modern phylogenetic techniques and molecular data, it is now understood that early classifications contained paraphyletic groups, which are no longer accepted. Modern classifications have greatly clarified the evolutionary relationships of the monocots. The widely-used Angiosperm Phylogeny Group (APG 2016) recognizes 78 families of monocots within 11 orders globally. An alternative treatment presented by Reveal (2012) incorporates a narrower circumscription, placing the monocots into 22 orders with 93 families. Table 2 provides a comparison of the two classification schemes (Reveal 2012; APG 2016) for the basal monocots covered in this flora.

Table 2. Comparison of APG (2016) and Reveal (2012) in their classifications of basal monocots treated in the flora of northern Alabama.

FAMILY	APG (2016)	Reveal (2012)
Acoraceae	Acorales	Acorales
Araceae	Alismatales	Arales
Tofieldiaceae	Alismatales	Tofieldiales
Alismataceae	Alismatales	Alismatales
Hydrocharitaceae	Alismatales	Alismatales
Zannichelliaceae*	Alismatales	Potamogetonales
Potamogetonaceae	Alismatales	Potamogetonales

* included in Potamogetonaceae by APG (2016)

For the purpose of this paper we follow APG's (2016) classification of orders and families. However, there has been a recent trend by some botanists (e.g., Reveal 2012, Weakley 2015, Keener et al. 2019) to recognize smaller, more narrowly defined families. While the family concepts used in this paper do not differ from APG (2016), subsequent treatments in the series are anticipated to deviate from their concepts; especially in the recognition of numerous segregate lilioid families (e.g., Weakley et al. 2015), which are broadly lumped in the most current version of APG (2016).

The order Acorales is represented by the monotypic family Acoraceae, with *Acorus* being the sole genus (APG 2016; Soltis et al. 2018) and *A. calamus* the only species in Alabama. The genus *Acorus* was traditionally classified as a member of the Araceae, but this was prior to the development of modern molecular and DNA sequencing techniques (Engler 1920; Cronquist 1981; Dahlgren et al. 1985). The taxonomy was based on a widespread assumption that the morphologically similar spadix and accompanying spathe-like leaf of *Acorus* were homologous to those same structures uniting the aroid plants (Grayum 1987; Thompson 1995, 2000a). However, despite the striking similarity in inflorescence types, *Acorus* was also believed to be highly aberrant in the Araceae (Grayum 1987).

Anatomical and embryological research on *Acorus* uncovered a wealth of data suggesting that its placement within the Arum family was incorrect. These early efforts discovered a number of unusual traits in *Acorus* that were atypical of the Araceae or completely absent from it, such as the

presence of a perisperm (a diploid food storage tissue in its seeds), ensiform (sword-shaped), unifacial (iris-like) leaves, and a lack of needle-like calcium-oxalate crystals, or raphides (Nicolson 1959; Kaplan 1970). Although the sheath-like bract of *Acorus* was previously interpreted to be equivalent to the spathe in Araceae, it has been shown to be independently derived (Ray 1987).

Morphological synapomorphies (shared derived traits) that might unite *Acorus* with some other group are ambiguous and its phylogenetic relationships remained unclear (Weakley 2015; Soltis et al. 2018). Despite its unresolved position, accumulating evidence from anatomical studies ultimately led to removing *Acorus* from Araceae and placing it into its own family, Acoraceae, and separate order, Acorales (Grayum 1987; Bogner & Nicolson 1991; Reveal 1995; Mayo et al. 1997; Takhtajan 1997; APG 1998; Reveal 2012). DNA analyses using multiple markers showed that *Acorus* is not only distinct from other members of the Araceae, but is a sister group to all other monocots (French & Kessler 1989; Duvall et al. 1993; Chase 2004; Graham et al. 2006).

APG (2016) divides the order Alismatales into 14 monophyletic families (Fig. 1). An alternative classification by Reveal (2012) employs smaller taxonomic entities, recognizing the following orders: Arales (Araceae), Tofieldiales (Tofieldiaceae), Alismatales (Alismataceae, Hydrocharitaceae), and Potamogetonales (Potamogetonaceae, Zannichelliaceae). Prior to DNA analyses, most authors, including Cronquist (1981), Dahlgren et al. (1985), and Takhtajan (1997), accepted a similarly coherent group of Alismatid-like monocots at some level. These botanists, however, consistently excluded aroid plants (i.e., Araceae, Lemnaceae, and Acoraceae), as well as the Tofieldiaceae, which was frequently included within Liliaceae.

Phylogenetic studies utilizing multiple DNA markers have shown that recognition of an expanded Alismatales including both Araceae and Tofieldiaceae, is phylogenetically warranted (Petersen et al. 2015; Luo et al. 2016; Soltis et al. 2018), with the latter family representing the order's most basal lineage (Luo et al. 2016). Alismatales is now viewed as sister to all other remaining monocots (excluding *Acorus*) (Ross et al. 2016; Soltis et al. 2018).

Families included within Alismatales share scales or glandular hairs at the nodes within their sheathing leaf bases, and their embryos are uniquely green (Soltis et al. 2018). The order contains one of the largest lineages of aquatic angiosperms — a clade of 12 exclusively aquatic families including free-floating, floating-leaved, submersed, and emergent taxa (Ross et al. 2016).

METHODS AND FORMAT OF FLORA

Northern Alabama (Fig. 2) includes all of the counties occurring within the Interior Plains and Appalachian Highlands. The two divisions encompass four physiographic provinces (Fenneman 1938): Interior Low Plateaus (Highland Rim section), Appalachian Plateaus (Cumberland Plateau section), Ridge & Valley (Tennessee section), and Piedmont Plateau (Piedmont Upland section).

County distribution maps with physiographic regions are provided for each species occurring within northern Alabama (Fig. 3). A symbol is used to document county-level occurrences within the physiographic province. In some cases more than one symbol per county is used. Specimens were examined from various herbaria and searches for collections were made online from the following sites: Alabama Plant Atlas (Keener et al. 2019), Floristic Synthesis of North America (Kartesz 2018), iNaturalist (2019), and the Southeast Regional Network of Expertise and Collections Data Portal (SERNEC 2018). All vouchered specimens were assessed from the following herbaria: ALNHS, AMAL, APSC, AUA, BRIT, CM, GA, F, FLAS, FSU, HTTU, IBE, JSU, KE, LSU, MICH, MUR, NCSC, NCU, NO, NY, SAMF, TENN, TROY, UCHT, UNA, UNAF, UWAL, and VDB. Herbarium acronyms follow those found in *Index Herbariorum* (Thiers 2016).

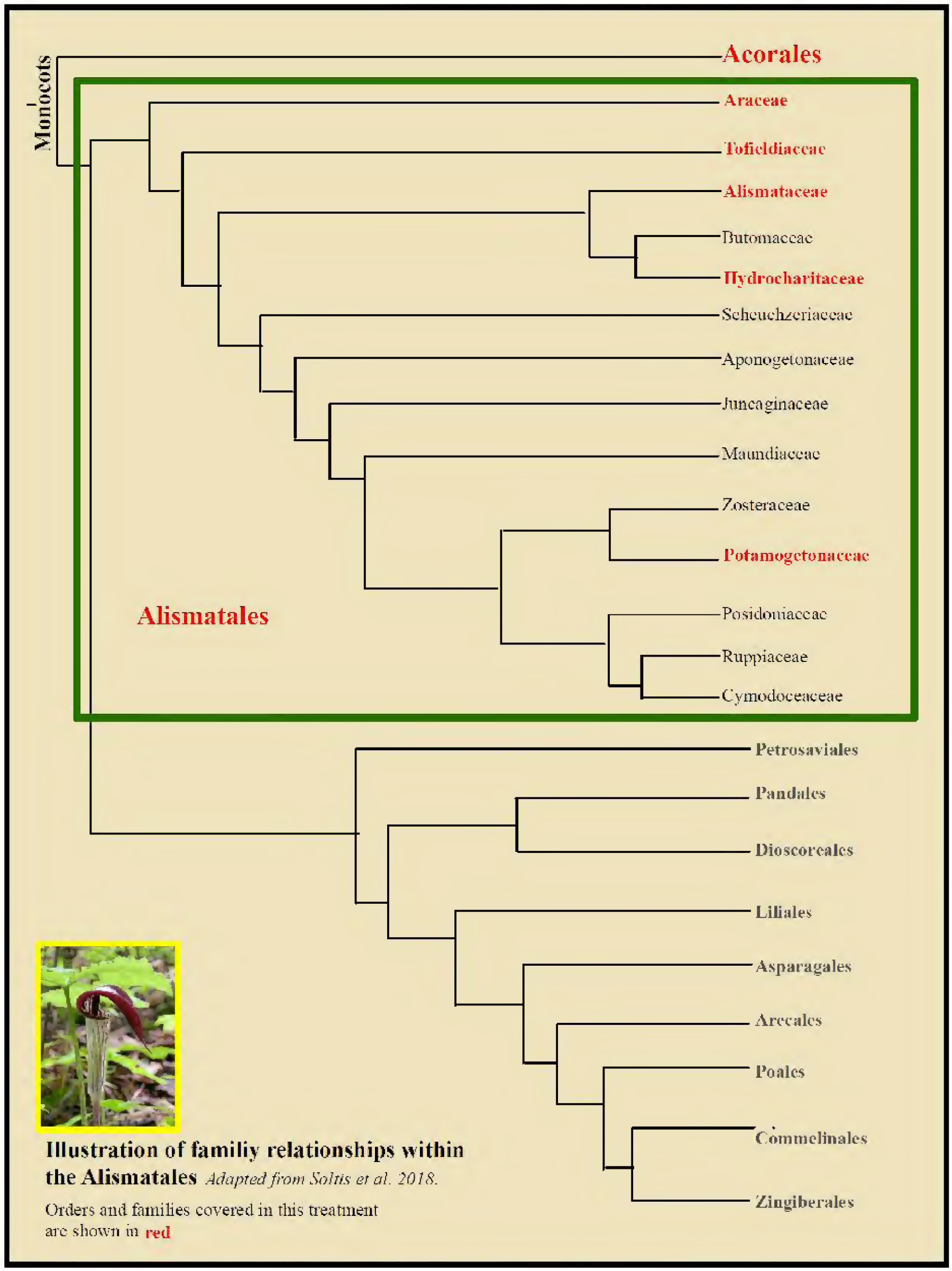


Figure 1. Phylogeny of the monocots showing the placement of Acorales and Alismatales.

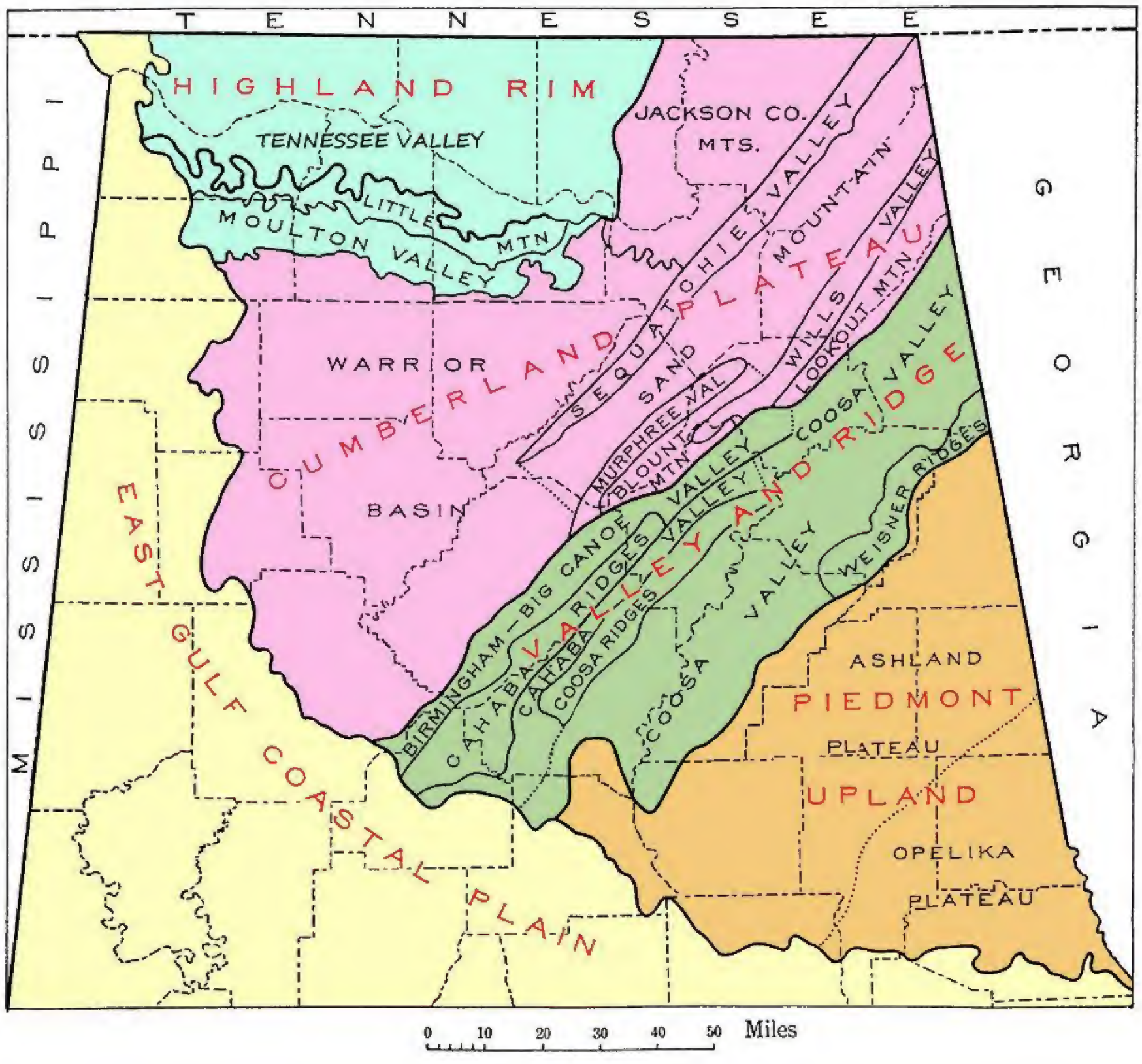
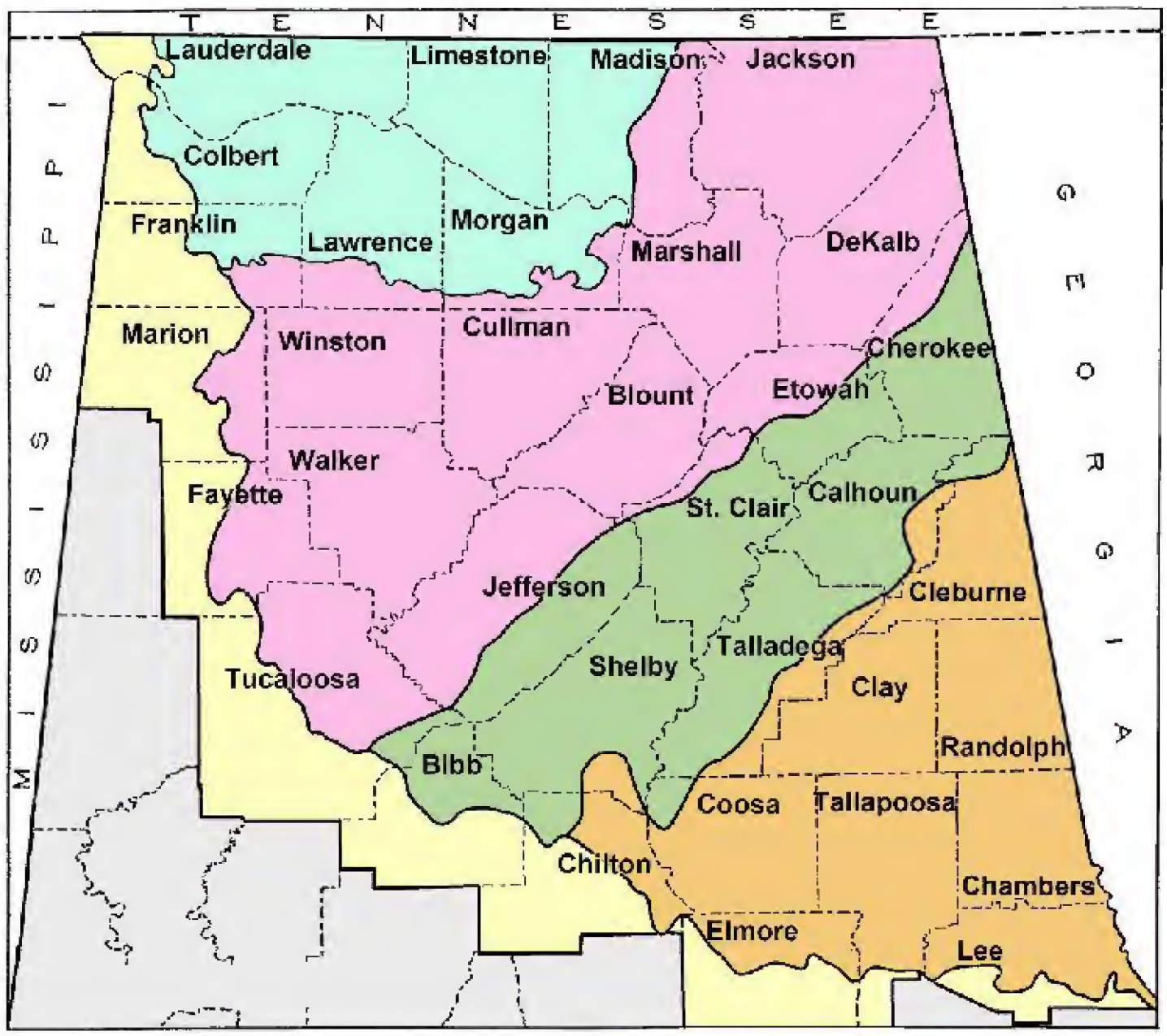


Figure 2. Map of physical divisions of northern Alabama (adapted and modified from Johnston 1930).

Family and generic sequences follow Weakley (2015) and are arranged phylogenetically, while species are arranged alphabetically. Generic names include authors and date of publication. The format for common names follows Kartesz (2018) and Kartesz & Thieret (1991). Within a given description of taxa the following sequence is followed: Scientific name, authority citation for specific and infraspecific taxa. Vernacular name(s). Synonyms. Habit/duration. Habitat. Flowering dates; fruiting dates (listed only if significantly different from flowering times). Frequency of occurrence in Alabama provinces. Overall range and distribution. Comments.

Frequency of occurrence is defined as follows, ranging in descending order: *Common* (occurring in abundance throughout a province); *frequent* (occurring throughout a province, but not abundant); *uncommon* (occurring in scattered localities in a province); *rare* (known only from a small number of populations, 6 to 20 occurrences, often restricted to specific localities or habitats); and *very rare* (known only from a few populations, 5 or fewer occurrences, often narrow endemics, disjuncts, or peripheral taxa, at the edges of their ranges).



MAP KEY	
●	Native taxon, present in physiographic area of county
✪	Sensitive species, listed as imperiled or rare in Alabama
▼	Exotic taxon, adventive or naturalized in Alabama

Figure 3. Counties of study area and map key to symbols

The following publications were utilized in creating keys: Abbott 2017; Armstrong 2001; Beal 1960; Clewell 1985; Cronquist 1981; Davenport & Haynes 1981; Diggs et al. 2006; Fassett 1940; Fernald 1950; Flora of North America Committee 2000; Godfrey & Wooton 1979; Haines 2011; Haynes 1977, 1978, 1979, 1980; Haynes & Holm-Nielsen 1987, 2001; Jones 2005; Landolt 1992; Meriläinen 1968; Mohlenbrock 1970; Radford et al. 1968; Rogers 1983; Small 1933; Smith 1994; Tennessee Flora Committee 2015; Wang et al. 2010; Weakley 2015; Wofford 1989; and Yatskievych 1999. Specimens were also examined from various southeastern herbaria, as well as recent collections in the field, to assist in construction of the keys.

KEY TO FAMILIES

1. Free-floating aquatic plants not rooted in substrate (occasionally stranded at low water.)

    2. Plants small thalloid bodies; leaves not distinct, reduced to fronds (< 2 cm long); roots present or absent .....**2. Araceae** (*Landoltia*, *Lemna*, *Spirodela, Wolffia, Wolffiella*)
    2. Plants much larger; leaves distinct in rosettes (> 2 cm long); roots present.

3. Leaves with petioles; leaf blades mostly cordate at base obtuse at apex; floating leaves with inflated cells (spongy tissue) underneath ..... **5. Hydrocharitaceae** (*Limnobium*)
3. Leaves sessile; leaf blades cuneate (wedge-shaped) at base, truncate at apex; floating leaves lacking inflated cells..... **2. Araceae** (*Pistia*)

1. Rooted terrestrial, amphibious, or submersed aquatic plants (unless uprooted or pieces broken off), a few species may have some floating leaves.

4. Plants submersed aquatics, though some leaves or stems may float on surface (sometimes stranded in substrate if water level is low); flowers emersed or submersed.

5. Leaves basally clustered.

6. Leaves flaccid and ribbon-like (of varying lengths, the longer ones often floating); pistillate flowers floating on long peduncles, staminate flowers submersed then later detach; carpels united ..... **5. Hydrocharitaceae** (*Vallisneria*)
6. Leaves firm, not ribbon-like (all roughly the same length, some with an expanded blade); flowers emersed or occasionally floating, but in 2 or more pedicelled whorls; carpels separate..... **4. Alismataceae** (*Sagittaria*)

5. Leaves scattered along stem.

7. Leaves opposite or alternate; carpels separate..... **6. Potamogetonaceae**
7. Leaves whorled; carpels united ..... **5. Hydrocharitaceae** (*Egeria*, *Elodea*, *Hydrilla*)

4. Plants terrestrial, amphibious, or an emersed aquatic, all or some of plant parts above water surface (base sometimes permanently submerged and some leaves occasionally floating); flowers emersed (aerial).

8. Leaves sessile, broadly linear, iris-like (leaves basally folded and partly enclosing the next leaf above).

9. Leaves >35 cm long and 5–18 mm wide; inflorescence lateral and sessile at base of leaf-like bract, 4–9 cm long (appearing to be an extension of the leaf) ..... **1. Acoraceae**
9. Leaves < 35 cm long and 1–6 mm wide; inflorescence racemose (with obvious glandular-pubescent peduncle), bracts minute, not leaf-like ..... **3. Tofieldiaceae**

8. Leaves petioled with expanded leaf blades, not iris-like.

10. Leaves compound, with 3 or more leaflets..... **2. Araceae** (*Arisaema*)
10. Leaves simple, not divided into leaflets.

11. Plants connected by stolons that are suspended in water; floating leaves suborbicular with a central disk of spongy, inflated cells underneath; flowers solitary in leaf axils. ..... **5. Hydrocharitaceae** (*Limnobium*)
11. Plant with or without stolons, if present, occurring at plant base, mostly in substrate, not suspended in water; floating leaves, if present, not suborbicular and lacking a central disk of spongy tissue (though some may be spongy throughout); flowers not solitary in leaf axils.

12. Leaf bases hastate, sagittate, or cordate, with distinct basal lobes.

13. Leaf blades with 3 prominent veins extending from the base to the tips of apex and lobes, smaller nerves branching off the main veins; apex and lobes of leaf broadly rounded or tapering to a rounded or obtuse tip; inflorescence a spadix subtended by a spathe (a sheathing bract); perianth absent ..... **2. Araceae** (*Arum*, *Colocasia*, *Peltandra*)
13. Leaf blades with numerous thick veins (more than 3) extending from base of blade to sides of lobes and apex; leaf apex and lobes sharply acute; inflorescence a raceme or panicle (with widely-spaced flowers on pedicels and in whorls); perianth consisting of white petals and green sepals ..... **4. Alismataceae** (*Echinodorus*, *Sagittaria*)

12. Leaf bases acute, obtuse, cuneate, truncate, rounded, or shallowly cordate, lacking obvious basal lobes.

14. Leaves blue-green with a velvety sheen and a water-repellent surface (water beading due to thick layer of short hairs); inflorescence a fleshy, elongated, bright golden-yellow to orange spadix; flowers crowded, sessile; perianth with yellow tepals.....**2. Araceae** (*Orontium*)
14. Leaves green, not water-repellent; inflorescence a diffuse raceme or panicle; flowers in widely spaced whorls; perianth with white petals and green sepals..... **4. Alismataceae** (*Alisma*, *Echinodorus*, *Sagittaria*)

FAMILY 1. ACORACEAE (Calamus Family)

1. ACORUS Linnaeus 1753

[Latin form of Greek *akoron*; ancient name of an aromatic plant]

1. Acorus calamus L. {old name for a reed} — COMMON SWEETFLAG; EUROPEAN CALAMUS; SWEETROOT; DRUG SWEETFLAG; FLAGROOT; CALAMUS-ROOT; SWEET-RUSH; SWEET-GRASS; SWEET-CANE; SINGLE-VEIN SWEETFLAG (Fig. 4). [*Acorus aromaticus* Gilib.; *Acorus calamus* var. *verus* L.; *Acorus calamus* var. *vulgaris* L.]

Figure 4. *Acorus calamus.* A. Inflorescence, Preble Co., Ohio, 28 May 2007. Photo: Daniel Nickrent. B. Population in ditch along margin of swamp, Cleburne Co., Alabama, 3 Apr 2019. Photo: Dan Spaulding.

Amphibious, perennial herb with rhizomes. Margins of springs, lakes, rivers, swamps, and marshes; flowers April–early August (sometimes populations produce none); rare in the Highland Rim, northeastern Cumberland Plateau, and lower Coastal Plain; very rare in the Ridge & Valley and Piedmont (Fig. 5). Early European settlers introduced a sterile triploid cytotype of *Acorus calamus* into North America (Thompson 2000a), which now occurs throughout the USA and adjacent Canada. Most populations are concentrated in the central and northeastern portions of the USA (Kartesz 2018). Common Sweetflag has been introduced world-wide in temperate regions (Grayum 1987).

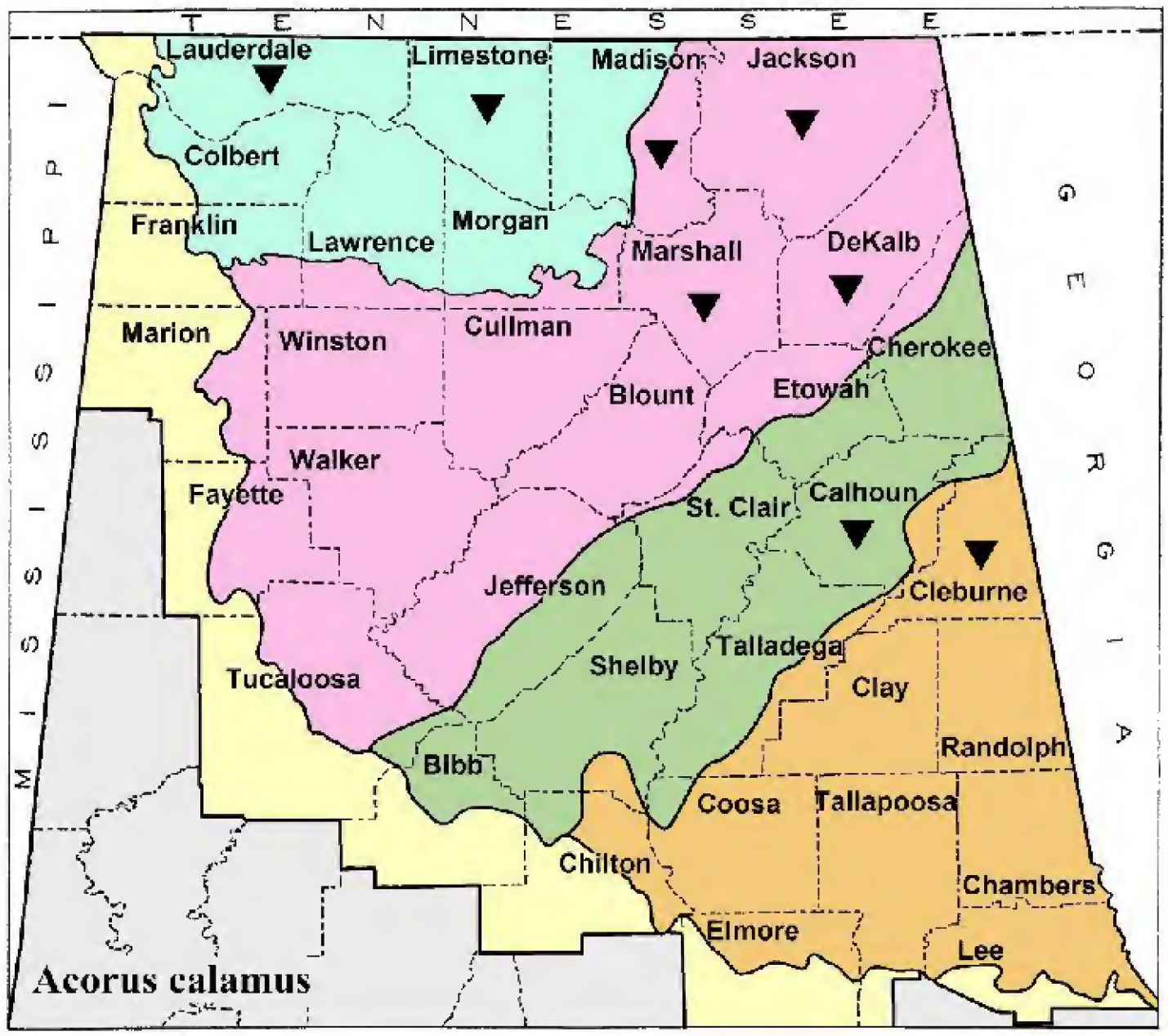


Figure 5. Distribution of *Acorus calamus* in northern Alabama.

According to Li et al. (2010), the triploid cytotype of *Acorus calamus* was created from a cross between diploid and tetraploid cytotypes that occur naturally in Asia. The authors asserted the triploid form may have originated in the Himalayan region and "then probably dispersed naturally or with humans to Sakhalin [large Russian Island] and with humans to Turkey, then to Europe, and finally to E North America as a medicinal plant."

Acorus is a small genus of two to six species (Grayum 1987). Li et al. (2010) concluded that only two species occurred worldwide: *A. calamus* and *A. gramineus* Sol. ex Ait. *Acorus gramineus*, Japanese Sweetflag, is native to eastern Asia and is commonly planted in the USA, but it is not known to escape. Japanese Sweetflag is easily recognized by its narrow (< 10 mm wide), non-aromatic leaves that lack a distinct midrib (Li et al. 2010).

Thompson (2000a) offered an alternative interpretation to the two-species concept. She recognized *Acorus americanus* (Raf.) Raf., a fertile diploid species restricted to the northern USA and adjacent Canada, as well as the sterile triploid plants *A. calamus*, introduced from the Old World.

Davenport and Haynes (1981) reported *A. americanus* from Alabama based on Wilson's (1960) assumption that *A. americanus* was the species represented in the southeastern USA. Wilson stated that "whether or not the European sterile triploid has been introduced into North America still remains to be shown." Thompson (1995) claimed that both taxa were present in North America and that our native plant was distinct from the Eurasian introduction. Thompson (2000a) concluded that *A. americanus* differs from *A. calamus* by having lateral veins as prominent as the midvein and its flowers produce fertile fruits, whereas *A. calamus* has only one prominent mid-vein and its flowers are sterile. However, Abbott (2016) suggested that *A. americanus* cannot be reliably separated morphologically on venation differences from *A. calamus* and said, "It is not yet clear that this global complex can be split into meaningful entities worthy of formal taxonomic recognition, or if it is just a complex based on ploidy-level differences."

(6a) Iris-like leaves, one prominent vein.

(6b) Rhizome of *Acorus*.

Figure 6. *Acorus calamus,* Salem Springs, Limestone Co., Alabama, 18 Jul 2018. Photos: Dan Spaulding.

Sweetflag has been used by various cultures for millennia. Its rhizomes produce essential oils that were utilized historically for numerous medicinal purposes. *Acorus* was found in Tutankhamen's tomb in Egypt and is mentioned in the Old Testament of the Bible (van Wyk & Wink 2004). Its aromatic leaves were also used by humans for other purposes. Dwyer et al. (1986) wrote that "settlers who knew the plant in Europe, where it was widely grown by the 17th century, scattered the lemony-smelling leaves on floors of their homes to mask the stench of poor sanitation and ventilation." The rhizome was candied (Coffey 1993) and reported to have been smoked or chewed to rid the taste of tobacco or to help break the habit (Dwyer et al. 1986). Caution is advised, however, since *Acorus* leaves (Fig. 6a) resemble some *Iris* species, which have poisonous rhizomes (Kingsbury 1964). In the New World, American Indians not only used the aromatic rhizomes (Fig. 6b) for medicinal purposes, but some tribes utilized the rootstalk as a medium of exchange (Dwyer et al. 1986). Native Americans may also have played a role in the distribution of the diploid form (Thompson 2000a).

FAMILY 2. ARACEAE (Arum Family)

The Araceae represent one of the most diverse flowering plant families in the world (Mayo et al. 1997; Christenhusz & Byng 2016). Members of the family have an inflorescence called a spadix, which consists of tightly packed, sessile flowers on a fleshy axis. The spadix is usually subtended or

enclosed by a leaf-like bract called a spathe. Plants in this family typically contain needle-like, calcium oxalate crystals within their tissues, which can cause an intense burning and are likely to inhibit consumption by herbivores (Wilson 1960).

As currently recognized (Reveal 2012; APG 2016), the Arum family is circumscribed to include the duckweed family (Lemnaceae). Previous recognition of duckweeds as a separate family was based on the group's diminutive size and accompanying reduction in reproductive structures, with flowers containing only simple pistils and anthers (Godfrey & Wooten 1979). Attesting to the extent of miniaturization, the duckweeds are known as the world's smallest angiosperms, with some individuals attaining a maximum width of only 0.3 mm at maturity (Landolt 1986).

Historically, Lemnaceae were suspected to be closely related to aroid plants (Cronquist 1981; Takhtajan 1997; Cabrera et al. 2008). Early anatomical and developmental studies were used to associate it with Araceae, in particular with the floating aroid genus *Pistia* (Grayum 1991; Cabrera et al. 2008). Modern molecular phylogenetic research has consistently shown that the Lemnaceae are clearly nested within Araceae and should be included within that family (French et al. 1995; Cabrera et al. 2008). Studies by Cabrera et al. (2008) revealed a more distant relationship between the duckweeds and *Pistia*. Their morphological similarities represent independent evolutionary origins that arose from adaption to an aquatic lifestyle.

1. Plants tiny, free-floating (rarely submersed), thalloid bodies (called fronds) < 2 cm long, (sometimes stranded in mud or on wet debris); leaves and stems reduced and cannot be differentiated; roots present or absent.

    2. Fronds lacking roots; veins absent.

        3. Fronds tiny (pinhead-sized), < 2 mm long, thick (at least below), globoid, ellipsoid, or ovoid, and a little longer than wide ..... **5. Wolffia**
        3. Fronds distinctly larger, > 3.5 mm long, flat, narrowly lanceolate, often falcate (sickle-shaped), and much longer than wide ..... **6. Wolffiella**

    2. Fronds with at least one root; veins one or more (though sometimes difficult to see).

        4. Frond with only 1 root; lower surface green or slightly reddish; upper surface entirely green; veins 1–3, but often obscure ..... **3. Lemna**
        4. Frond usually with 2 or more roots (a few fronds rarely with one); lower surface often solid reddish-purple; upper surface completely green or green with a purple margin; veins 3 or more, some often easily discernable.

            5. Roots (6-) 7–18 (-21); fronds nearly as wide as long, usually broadly obovate, or orbicular-ovate with main frond 5–10 mm long (daughter fronds smaller); upper surface often with a red or purple dot near end of frond, where roots attach; veins of frond mostly 5–16 ..... **2. Spirodela**
            5. Roots usually (1-) 2–5 (-7); fronds typically longer than wide, usually obovate, narrowly obovate, or oblong-ovate, with main fronds 2–5 mm long; upper surface lacking a single, conspicuous red dot, but can punctate with scattered reddish-brown pigment cells; veins mostly 3–5 ..... **4. Landoltia**

1. Plants much larger, either emergent or free-floating aquatics; leaves and stems distinct (except *Pistia*, which lacks a discernible stem); roots present.

6. Floating aquatic plants; leaves in cabbage-like rosettes; blades densely pubescent and obovate, with a cuneate base and truncate apex; roots conspicuously feathery and clustered beneath the rosette of leaves; stems absent..... **8. Pistia**
6. Rooted terrestrial or aquatic plants; leaves and roots not as described above; stems present.

    7. Leaves compound, with 3 or more leaflets; plant arising from a corm (swollen bulbous base) that lacks stolons ..... **10. Arisaema**
    7. Leaves simple, undivided; plant with rhizomes, tubers, or stoloniferous corms.

        8. Leaf bases tapering (acute or cuneate); blades oblong-elliptic or lanceolate; spadix golden yellow and not enclosed in a spathe; perianth consisting of 6 yellow tepals; main veins of leaves parallel..... **1. Orontium**
        8. Leaf bases cordate, hastate, or sagittate; blades cordate-hastate, ovate-triangular, hastate, or sagittate; spadix greenish or whitish and enclosed in a spathe; perianth absent; main veins of leaves palmate or pinnate, not parallel.

            9. Leaves peltate (petiole attached on the undersurface of leaf, not at margin of blade); basal leaf lobes obtuse or broadly rounded ..... **9. Colocasia**
            9. Leaves not peltate (petiole attached on the margin of leaf at base of blade); basal leaf lobes acute or tapering to an obtuse apex.

                10. Leaves green throughout; base of spadix not sessile; terminal portion of spadix lacking a sterile appendix or reduced to only a few millimeters in length; berries green at maturity, remaining enclosed within spathe; leaves present when fruiting; native wetland plant lacking tubers..... **7. Peltandra**
                10. Leaves variegated with conspicuous whitish veins; base of spadix narrowed below forming a stalk; terminal portion of spadix with a conspicuous sterile appendix; berries red at maturity, not enclosed within the spathe (it withers away); leaves die back during fruiting; alien terrestrial plant with tubers..... **11. Arum**

1. ORONTIUM Linnaeus 1753

[Ancient name of a plant said to have grown in the Syrian river Orontes]

1. Orontium aquaticum L. {aquatic} — GOLDEN-CLUB; BOG-TORCH; NEVER-WET (Fig. 7).

Amphibious to emersed, perennial herb with rhizomes. Marshes, swamps, bogs, lakes, streams, and rivers; flowers February–May, fruits May–July; rare in the Highland Rim (Little Mountain district); uncommon in the Cumberland Plateau, Ridge & Valley, and Piedmont; frequent in the Coastal Plain (Fig. 8). *Orontium* is a monotypic genus, endemic to the eastern USA and occurs primarily on the southeastern Coastal Plain (Wilson 1960), but it extends inland into the other physiographic provinces within suitable habitats (Grear 1966). The species is native from New York and Massachusetts south to Florida, west to Kentucky and eastern Texas (Kartesz 2018).

Orontium aquaticum prefers acidic sandy, muddy, or peaty soils (Klotz 1992). It frequently inhabits shallow waters (Fig. 9a), but if water is low it can grow in wet substrates (Fig. 9b). When water levels are high, its leaves will often float, due to large intercellular air spaces in the leaves (Thompson 2000b). Populations of *Orontium* can be dense and expansive (Fig. 10a), especially on the Coastal Plain, but in the Appalachians individuals may occur lodged within cracks in sandstone bedrock of streams (Fig. 10b).

Figure 7. *Orontium aquaticum*, Perry Co., Alabama, 7 Apr 2015. Photo: Brian Finzel.

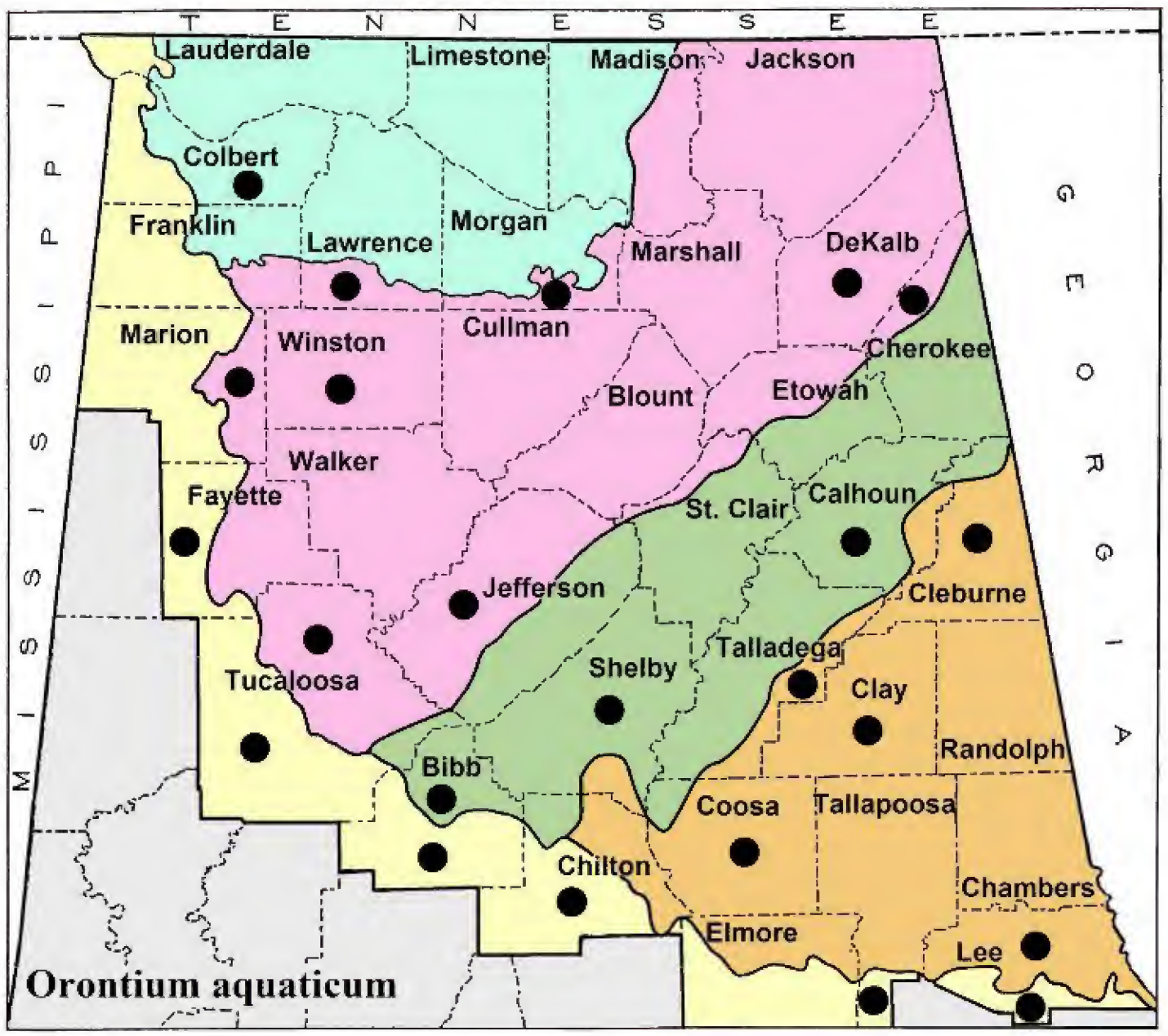
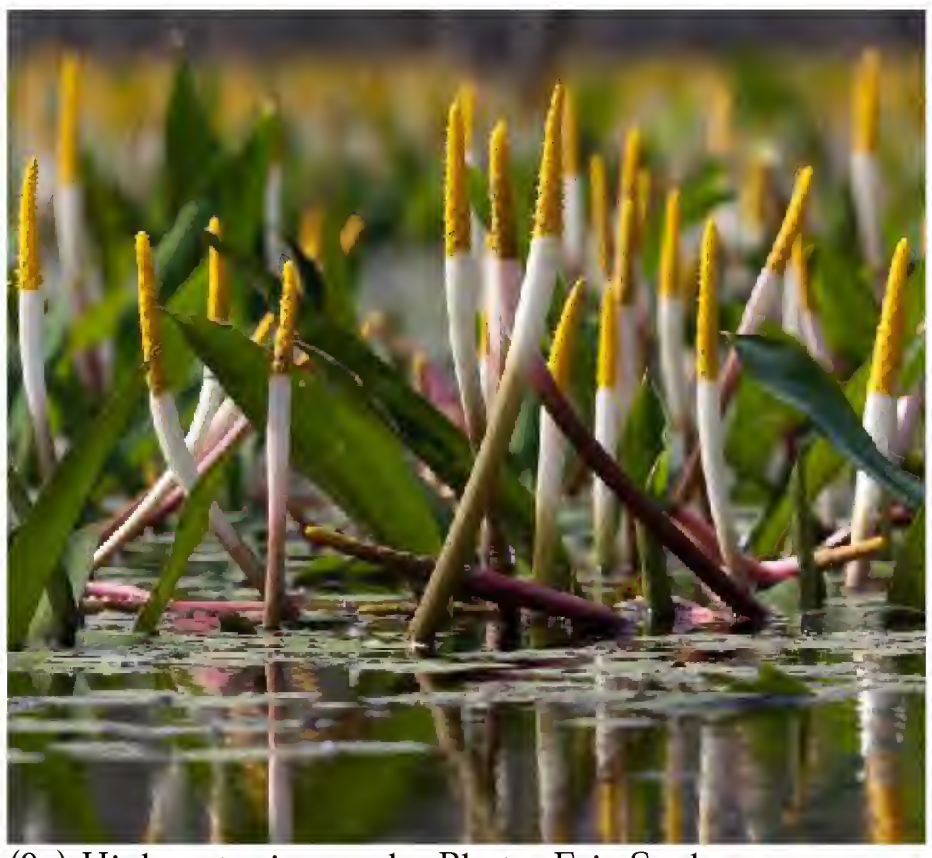


Figure 8. Distribution of *Orontium aquaticum* in northern Alabama.

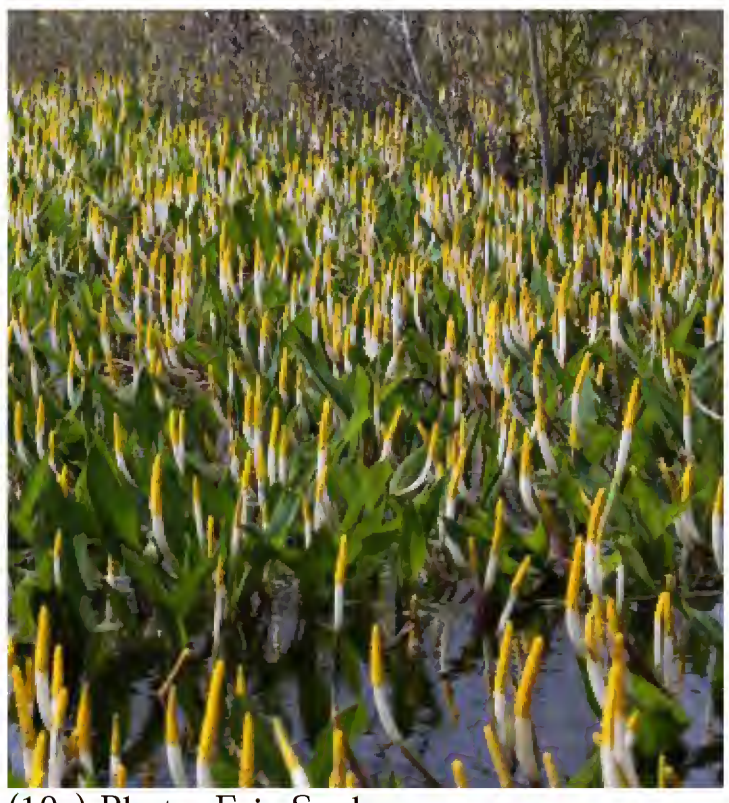
Golden-Club is a very distinct species with a golden yellow-orange spadix that is not enclosed by a spathe (a leaf-like bract). The spadix is a fleshy spike of crowded flowers, initially green, turning brilliant yellow at maturity, then becoming green again following pollination. The flower stalk (scape) grows downward following pollination, with most fruits (Fig. 10c) maturing underwater. When the berry-like fruits ripen, they detach from the spadix and float. Buoyancy is due to air spaces within the seed coat (the pericarp). The fruit will float on the surface for about a week, then sinks after becoming water-logged. The seeds are dispersed by water or animals (Klotz 1992).



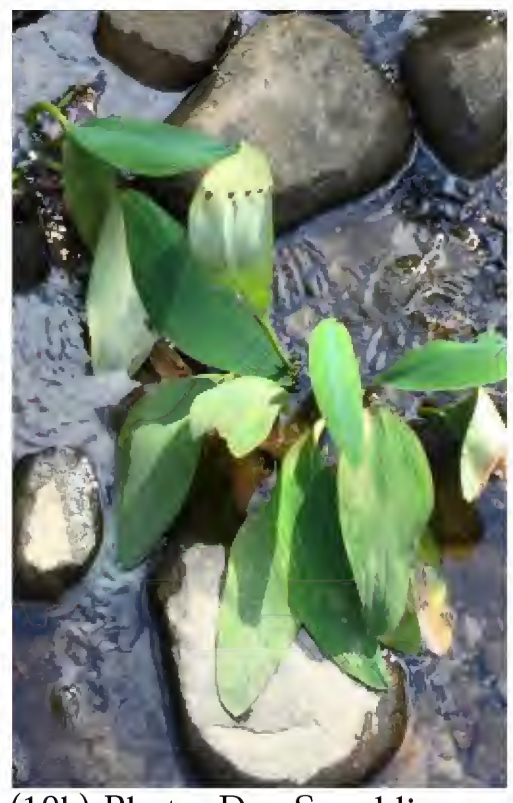
(9a) High water in marsh. Photo: Eric Soehren.

(9b) Ebenezer Swamp. Photo: Brian Finzel.

Figure 9. *Orontium aquaticum*. A. Mobile Co., Alabama, 7 Apr 2010. B. Shelby Co., Alabama, 28 Mar 2016.



(10a) Photo: Eric Soehren.



(10b) Photo: Dan Spaulding.

(10c) Photo: Brian Finzel.

Figure 10. *Orontium aquaticum*. A. Backwaters of Escatawpa River, Mobile Co., Alabama, 7 Apr 2010. B. Little River, Cherokee Co., Alabama, 14 Oct 2018. C. Unripe fruits, Perry Co., Alabama, 27 May 2013.

This species is easily identified by its unlobed, blue-green, elliptical leaves that have a velvety sheen. The blades are protected by a waxy epidermal cell layer and covered by short hairs, which in combination makes their surfaces appear to be "unwettable" (Thompson 2000b). Davenport

and Haynes (1981) reported "that water will run off or bead up rather than wet the leaves." When fresh foliage is submersed, it becomes silvery iridescent but once removed appears to be completely dry, hence the name "Never-Wet" (Grimm 1968). In autumn, the leaves wither and the plant becomes dormant until the following spring. Native Americans used the starchy seeds and rhizomes for food, but they first had to boil and dry them to remove irritating calcium oxalate crystals (Klotz 1992). The rhizome was ground into a nutritious, mealy flour and the seeds were eaten as a pea-like vegetable (Peterson 1977).

2. SPIRODELA Schleiden 1839

[Evident cord; possibly alluding to the roots]

1. Spirodela polyrrhiza (L.) Schleid. {many-rooted} — GREATER DUCKWEED; MINNOW-FOLE; COMMON DUCKMEAT (Fig. 11).

Figure 11. *Spirodela polyrrhiza,* swamp in Bullock Co., Alabama, 18 May 2018. Photo: Dan Spaulding.

Floating aquatic, perennial herb. Marshes, swamps, inlets, lakes, sloughs, ponds, and still waters of streams, rivers, and creeks; rarely flowers and fruits in early summer–early fall (Landolt 2000); uncommon in the Highland Rim and Cumberland Plateau; rare in the Ridge & Valley and Piedmont; frequent in the Coastal Plain (Fig. 12). Inhabiting eutrophic, quiet waters in temperate and tropical regions nearly worldwide (Landolt 2000).

Spirodela polyrrhiza is the largest duckweed in Alabama, with more roots than any other species. Its fronds are broadly obovate to suborbicular, purplish underneath, green above, with usually 7–16 palmately arranged veins. The upper surface is typically red-dotted near the apex where roots attach below. This character is due to the accumulation of reddish pigments (anthocyanin) caused by the reduction of nutrients (Bog et al. 2015). When waters are nutrient dense (e.g., agricultural ponds) the colored spot is frequently lacking (Fig. 13).

Flowers of *Spirodela* are enclosed within a membranous spathe within a reproductive pouch along the margin of the frond. Reproduction, however, is mostly vegetative because it rarely flowers (Wilson 1960). Populations emerge via production of new fronds that emerge through slits in the sides of parent fronds. *Landoltia* is a similar duckweed but has smaller, narrowly obovate fronds (Fig. 14a). *Spirodela* has more numerous roots (Fig. 14b) and produces turions (Fig. 14c), disk-

shaped "resting fronds" loaded with starch that sink to the bottom and remain dormant throughout winter (Dölger 1997). Turions are absent in *Landoltia punctata* (Les & Crawford 1999).

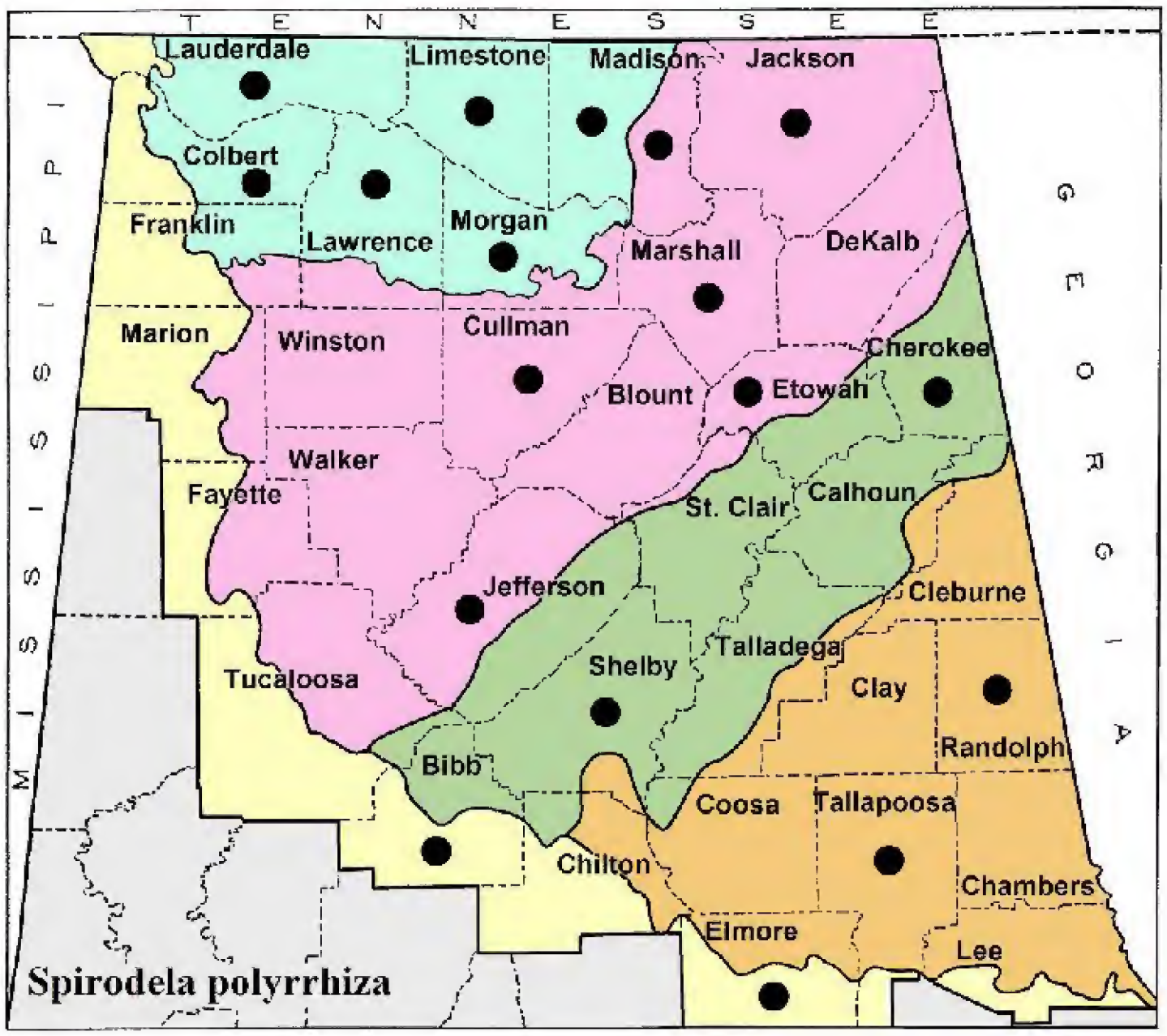


Figure 12. Distribution of *Spirodela polyrrhiza* in northern Alabama.

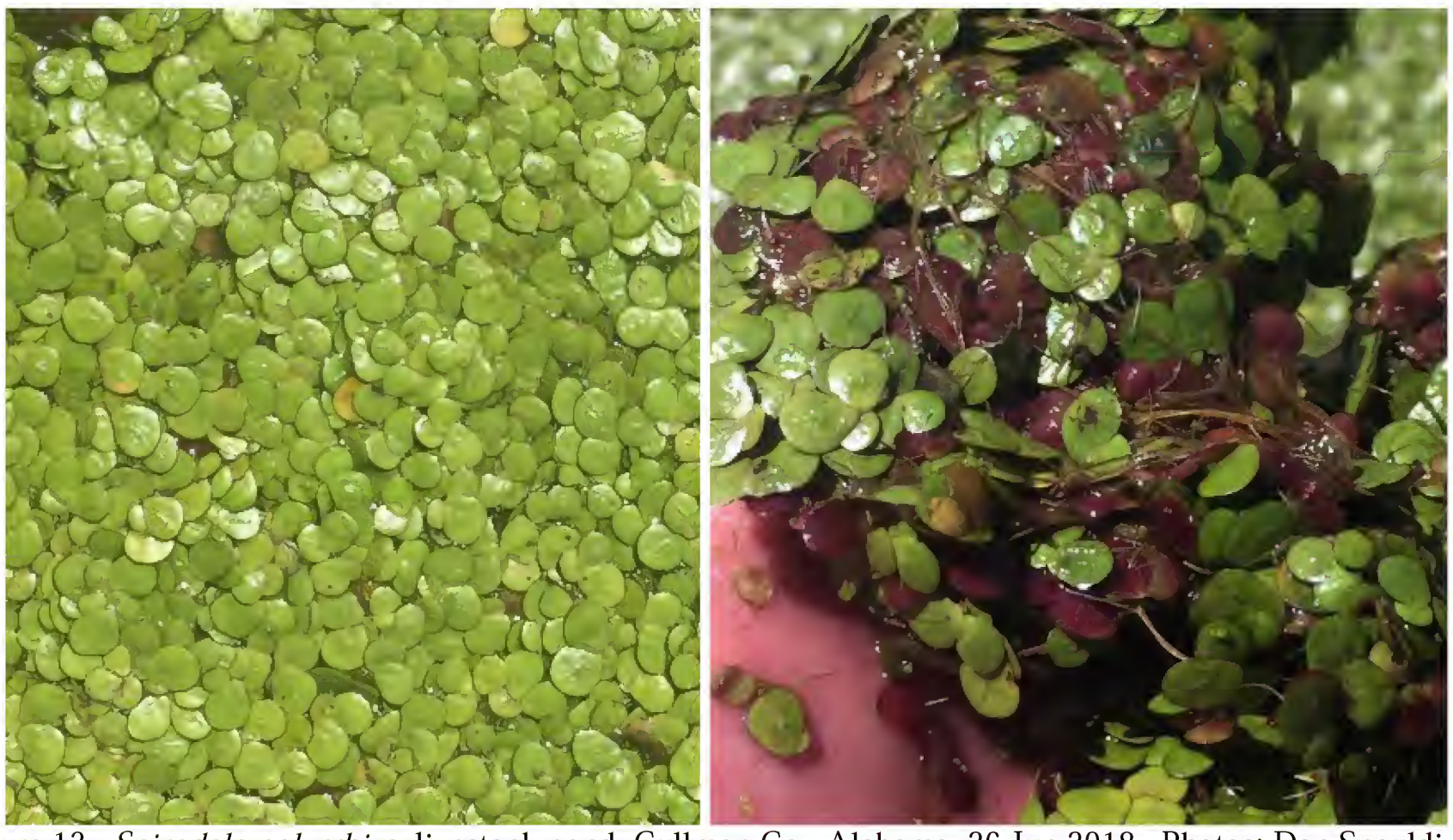
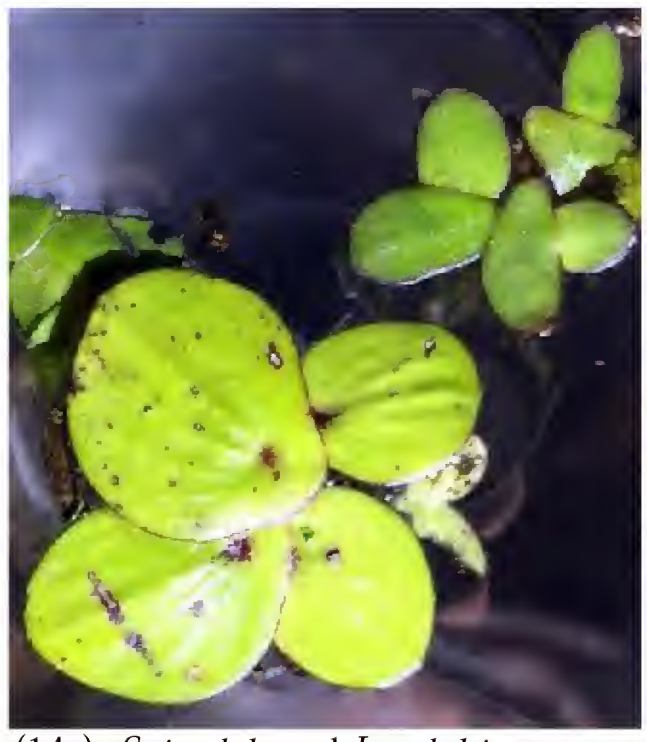
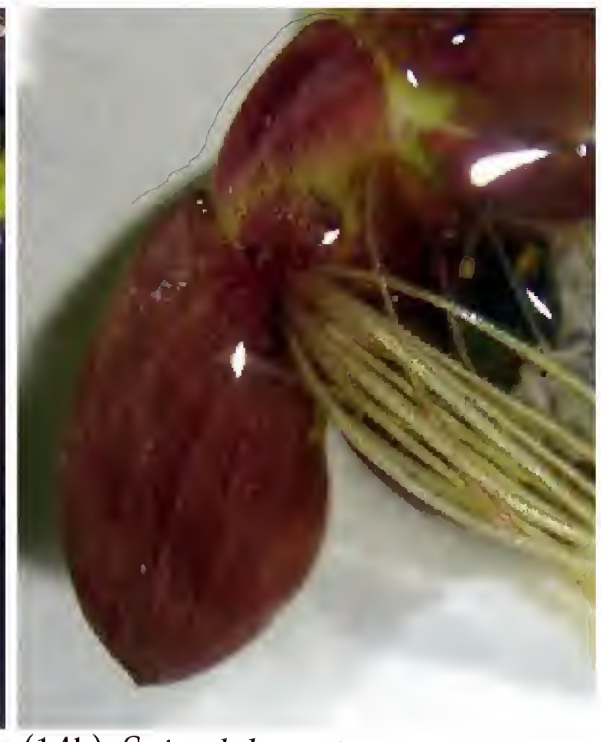


Figure 13. *Spirodela polyrrhiza*, livestock pond, Cullman Co., Alabama, 26 Jun 2018. Photos: Dan Spaulding.



(14a) *Spirodela* and *Landoltia.*



(14b) *Spirodela* roots.

(14c) *Spirodela* turion.

Figure 14. A. Weiss Lake, Cherokee Co., Alabama, 20 Jun 2018. B. Swamp, Bullock Co., Alabama, 18 May 2018. C. Farm pond, Cullman Co., Alabama, 26 Jun 2018. Photos: Dan Spaulding.

3. LEMNA Linnaeus 1753
[Ancient name of an aquatic plant]

Duckweeds are much easier to key when fresh. Once dried, fronds may need to be rehydrated to make an accurate determination. Armstrong (2001) recommends that "herbarium specimens of duckweeds be soaked (hydrated) in a small container of water. This allows the tissues to absorb (imbibe) water, enabling certain characteristics discernible under a dissecting microscope. It is also preferable to examine them using background lighting or a white background to observe the number of veins and other diagnostic features." Staining the fruits with a red dye and placing them on a transparent slides is also helpful (Yatskievych 1999). Due of the difficulty in discerning veins and minute surface features on the fronds, these characters should not be solely relied upon in order to make determinations.

1. Fronds narrowly elliptic, oblong, narrowly ovate, linear, or lanceolate; sides of fronds are typically asymmetric or basally oblique; both surfaces green; veins 1 ..... **3. *Lemna valdiviana***
1. Fronds oval to broadly elliptic; sides of fronds mostly symmetrical and base not oblique; surfaces green or lowers surface sometimes with reddish pigmentation; veins 3–5 (often very obscure).
    2. Roots not longer than 3 cm long; root tip usually sharply pointed; sheath of root winged basally (best seen when fresh under high magnification); frond lacking any reddish pigmentation ..... **1. Lemna aequinoctialis**
    2. Roots > 3 cm (up to 15 cm long); root tip mostly rounded; sheath of root not winged basally; fronds occasionally with reddish pigmentation (especially on the lower surface where the root attaches) ..... **2. Lemna obscura**

1. Lemna aequinoctialis Welw. {of equatorial regions} — LESSER DUCKWEED; THREE-NERVE DUCKWEED (Fig. 15). [*Lemna trinervis* (Austin) Small]

Floating aquatic, perennial herb. Still or slow moving water of ponds, swamps, streams, inlets, creeks, lakes, ditches, and man-made tanks or containers. Flowers and fruits generally develop in early summer–early fall (Landolt 2000). Frequent in the Highland Rim, Cumberland Plateau,

Ridge & Valley, and Coastal Plain; infrequent in the Piedmont (Fig. 16). Widespread worldwide, except in northern regions of North America and Eurasia (Weakley 2015).

Figure 15. *Lemna aequinoctialis*, small tributary to Choccolocco Creek, below a beaver dam, Talladega Co., Alabama, 22 Apr 2019. Photo: Dan Spaulding.

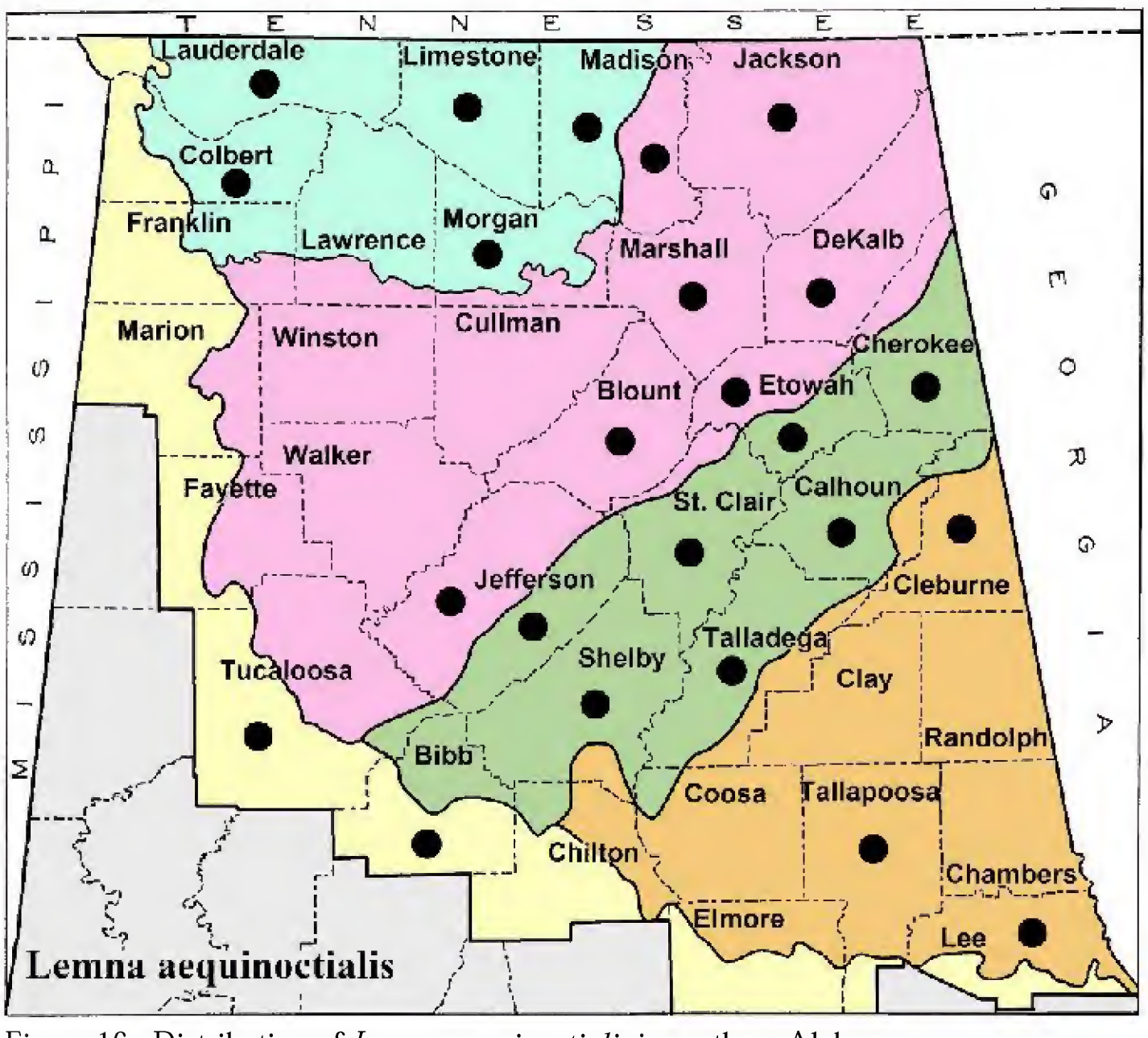


Figure 16. Distribution of *Lemna aequinoctialis* in northern Alabama.

Lemna aequinoctialis is similar to *L. obscura* but has a winged root sheath (Fig. 17a) and shorter roots (< 3 cm long) with sharp-pointed tips (Fig. 17b–c). *Lemna aequinoctialis* is the only annual duckweed known from Alabama. Viable, fertile fruits help to spread the species into new locations. Davenport and Haynes (1981) reported another annual, *L. perpusilla* Torr. (Minute Duckweed) for Alabama, but no specimens were seen in our study. Some authors place *L. aequinoctialis* into synonymy under *L. perpusilla* (Daubs 1965), but these two species can be identified by their seeds and surface features of their fronds (Weakley 2015). *Lemna perpusilla* has whitish seeds with 35–70 obscure ribs and its fronds have 2–3 papillae above the node, which are larger than the papule at the apex. *Lemna aequinoctialis* has brownish seeds with 8–26 prominent ribs and its fronds have only 1 papilla above the node, which is smaller than the papule at the apex.

(17a) Winged root sheath.

(17b) Root < 3cm with pointed tip.

(17c) Fronds with shorter roots.

Figure 17. A–B. Fronds growing in swamp by Choccolocco Creek in Talladega Co., Alabama, 13 May 2018. C. Crystal Springs, Calhoun Co., Alabama, 8 Jun 2018. Photos: Dan Spaulding.

2. Lemna obscura (Austin) Daubs {hidden} — LITTLE DUCKWEED (Fig. 18). [*Lemna minor* L. var. *obscura* Austin]

Figure 18. *Lemna obscura*, Salem Springs, Limestone Co., Alabama, 15 Jul 2018. Photo: Dan Spaulding.

Floating aquatic, perennial herb. Still or slow moving water of rivers, lakes, marshes, swamps, ponds, springs, and man-made ponds; occasionally flowers and fruits spring–fall (Landolt 2000); frequent in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Coastal Plain;

infrequent in the Piedmont (Fig. 19). Native to the New World in temperate and subtropical regions with mild winters, from the USA south to Columbia and Ecuador (Landolt 2000).

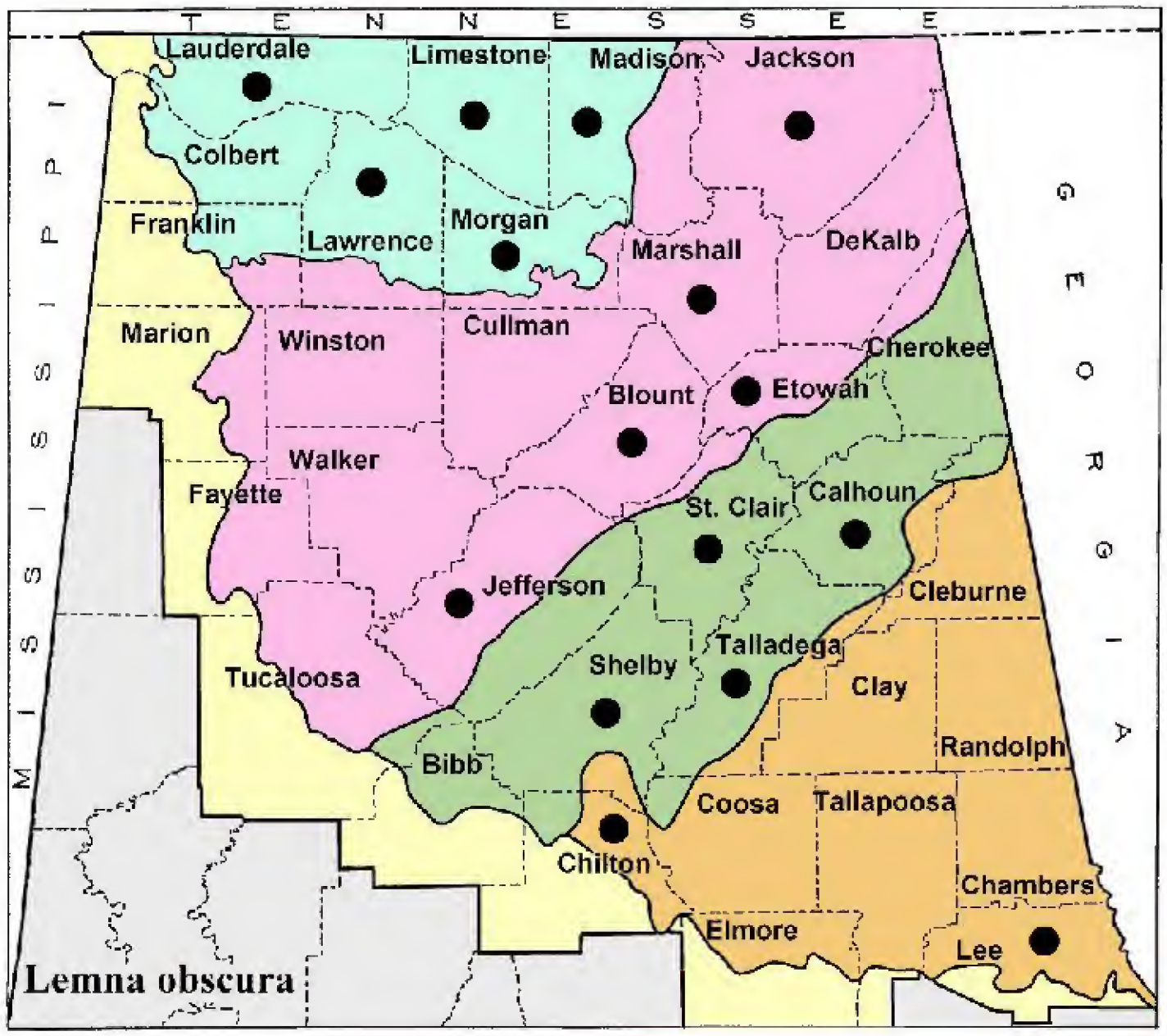


Figure 19. Distribution of *Lemna obscura* in northern Alabama.

Lemna obscura is similar to *L. aequinoctialis* but has longer roots (up to 15 cm), which often form a tangled hair-like mass (Fig. 18). Other distinguishing characters include the root tip being rounded rather than sharply pointed (Fig. 20a), a root sheath that is not winged, and lower surface of fronds being reddish or sometimes green (Fig. 20b–c).

(20a) Round root tip.

(20b) Fronds red or green beneath.

(20c) Fronds sometimes blotched with red.

Figure 20. *Lemna obscura*. A. Pond, Calhoun Co. Alabama, 29 Mar 2018. B. Tennessee River, Lawrence Co., Alabama, 20 Aug 2018. C. Lay Lake, Chilton Co., Alabama, 19 Jul 2018. Photos: Dan Spaulding.

Lemna turionifera Landolt [Turion Duckweed] was reported from Jackson County in northeast Alabama (Kartesz 2018; Landolt 2000), but no specimens were seen. This species has small, flat olive-brown fronds with papillae on midline of the upper surface. Turion Duckweed often produces small, rootless turions (0.8–1.6 mm in diameter) that sink to the bottom in the fall (Fig. 21). *Lemna obscura* differs by lacking turions and having mostly gibbous ("hump-backed") fronds with papillae above the node, near the apex of the upper surface (Weakley 2015).

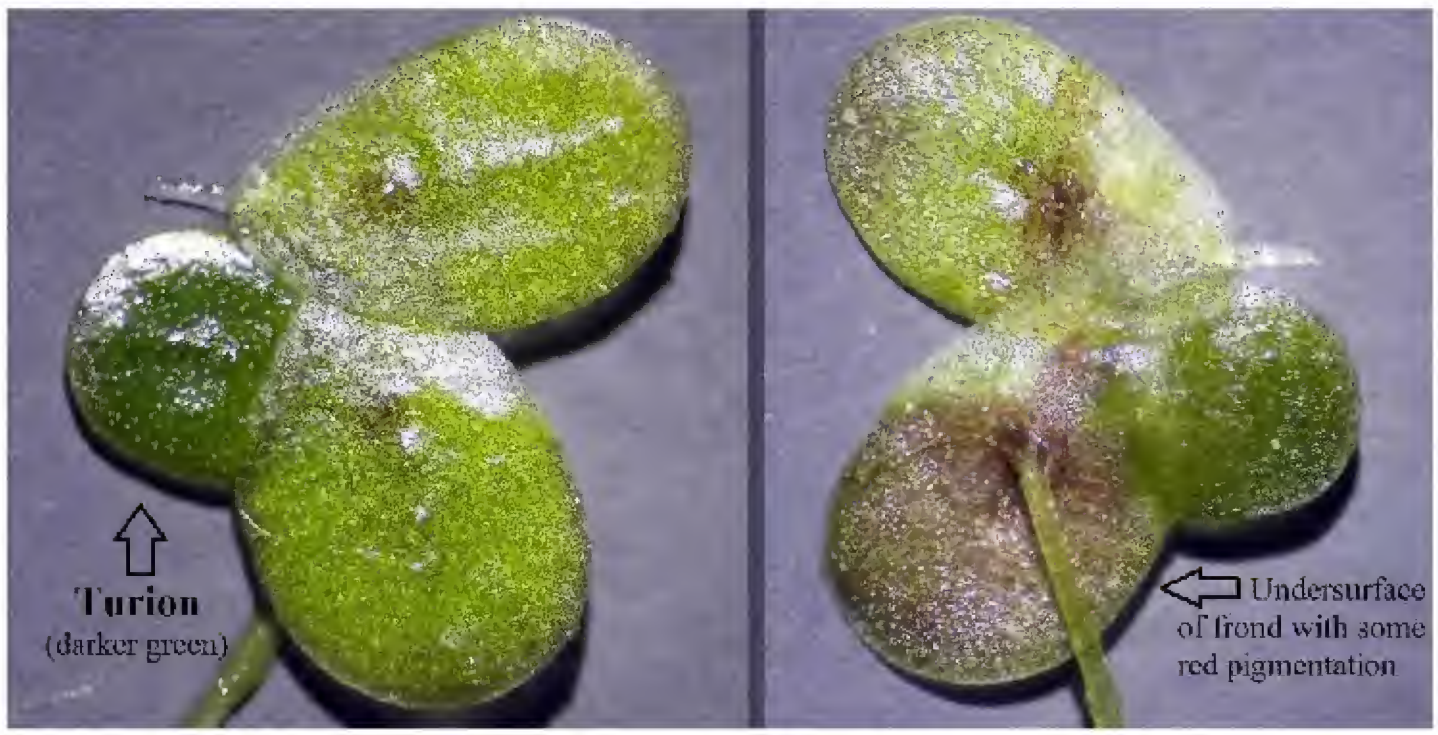


Figure 21. *Lemna turionifera*, backwaters of Danube River, Austria, 3 Oct 2016. Photo: Stefan Lefnaer.

Lemna minor (Fig. 22) is also similar to *L. obscura*, but no valid specimens were observed in this study. Landolt (2000) listed it for Alabama, with collections reported from several counties (Kartesz 2018; SERNEC 2018). Davenport and Haynes (1981) said *L. minor* was "common in ponds and logjams throughout the State." It is possible that many reports of *L. minor* have been misapplied to *L. obscura* in Alabama. Austin (1867) first described this taxon as *L. minor* var. *obscura*, but Thompson (1898), in his revision of American Lemnaceae, did not recognize it. However, Daubs (1965) justified elevating Austin's variety to species rank, because of its larger, gibbous fronds that are often more pigmented than those of *L. minor*. Additionally, the upper surface of *L. obscura* fronds have a prominent papule near the apex with a row of distinct papules along the midvein, whereas the fronds of *L. minor* have papules that are all relatively small (Yatskievych 1999). Turions are absent in both these species, but daughter fronds can be confused for turions, but they are the same color or lighter than parent fronds and also develop roots when mature.

Figure 22. *Lemna minor*, pond in Austria, 28 Aug 2018. Photo: Stefan Lefnaer.

3. Lemna valdiviana Phil. {of Valdivia, Chile} — VALDIVIA DUCKWEED; PALE DUCKWEED; SMALL DUCKWEED (Fig. 23).

Figure 23. *Lemna valdiviana*, Borden Springs, Cleburne Co., Alabama, 9 Jun 2018. Photos: Dan Spaulding.

Floating aquatic, perennial herb. Still or very slow moving water of swamps, marshes, ponds, rivers, inlets, lakes, streams, creeks, and springs; rarely flowers and fruits in spring–fall (Landolt 2000); infrequent in the Highland Rim, Cumberland Plateau, and Coastal Plain; rare in the Ridge & Valley (Fig. 24). Native to temperate and tropical regions of the USA south to South America (Landolt 2000).

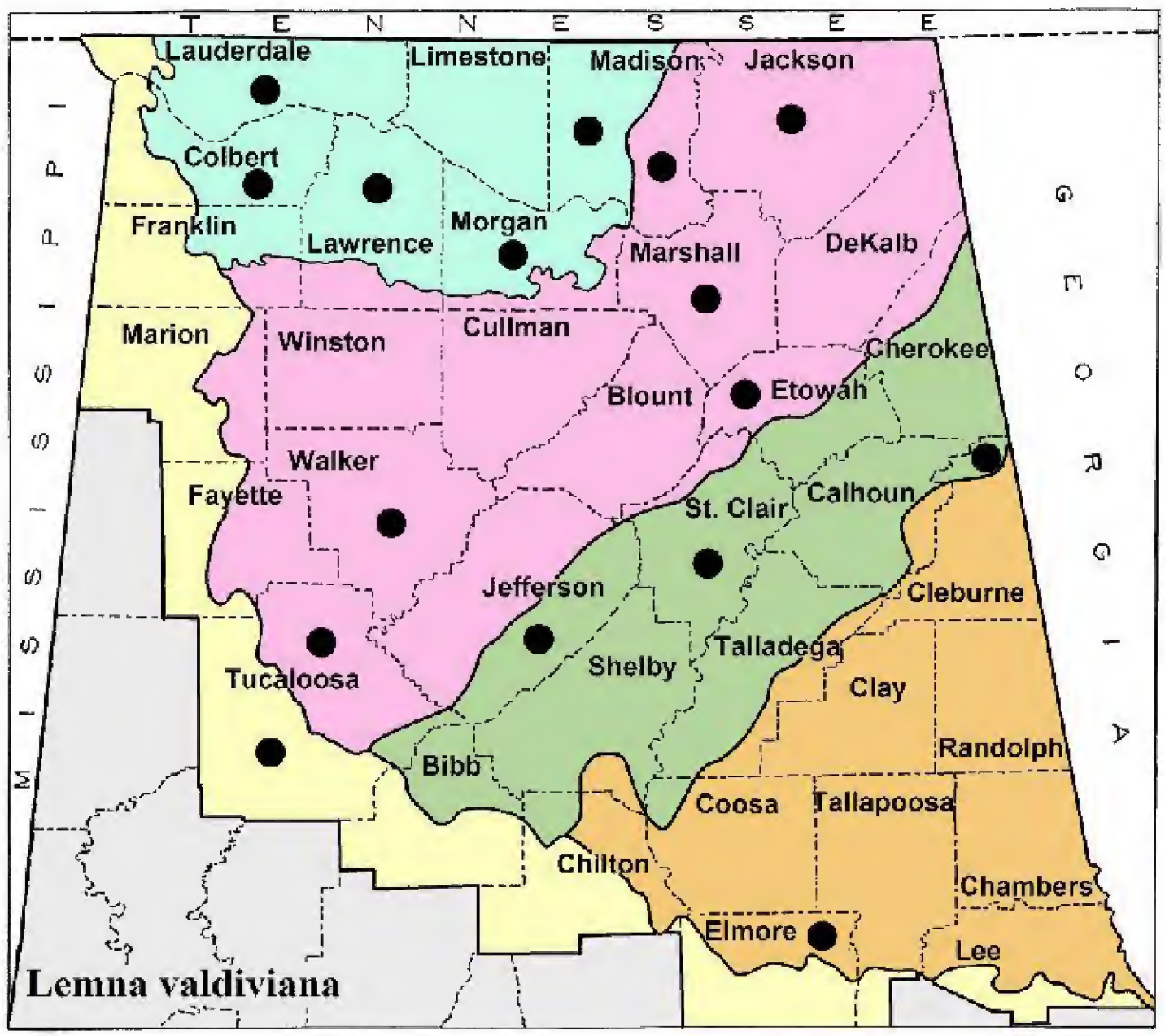


Figure 24. Distribution of *Lemna valdiviana* in northern Alabama.

Lemna valdiviana is very distinctive, its fronds are asymmetrical basally, up to 3 times longer than wide, mostly 2.5–5 mm long, and either floating or occasionally submersed. When this duckweed's fronds are connected in 4s they often resemble a butterfly (Fig. 25).

Figure 25. *Lemna valdiviana* fronds, Cleburne Co., Alabama, 9 Jun 2018. Photo: Dan Spaulding.

Lemna valdiviana is similar to *L. minuta* Kunth [Least Duckweed] because both have single veined fronds. *Lemna minuta* has been reported for Alabama (Kral et al. 2011) from Colbert, Houston, and Jackson counties (Keener et al. 2019). Northern Alabama collections have been annotated to *L. valdiviana* and visits to the site in Houston County found only *Landoltia punctata*. The fronds of *L. minuta* (Fig. 26) are nearly symmetrical basally, 1–2 times longer than wide, mostly 1–3 mm long, and are always found floating (Diggs et al. 2006).

Figure 26. *Lemna minuta* with *L. minor*, France, 30 Apr 2016. Photo: Pascale Guinchard.

4. LANDOLTIA D.H. Les & D.J. Crawford 1999

[Named for Elias Landolt, 1926–2013, a duckweed expert from Zurich, Switzerland]

1. Landoltia punctata (G.F.W. Mey.) D.H. Les & D.J. Crawford {dotted} — DOTTED DUCKMEAT; DOTTED DUCKWEED; LESSER GREATER DUCKWEED (Fig. 27). [*Lemna punctata* G.F.W. Mey.; *Spirodela oligorrhiza* (Kurz) Hegelm.; *Spirodela punctata* (G.F.W. Mey.) Thomps.]

Figure 27. *Landoltia punctata*, marsh in Lee Co., Alabama, 29 May 2018. Photo: Dan Spaulding.

Floating aquatic, perennial herb. Still or slow moving water of ponds, lakes, swamps, springs, marshes, inlets, rivers, streams, livestock watering holes, man-made water tanks, and water treatment lagoons; rarely flowers and fruits in summer–early fall (Landolt 2000); uncommon in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Piedmont; frequent in the Coastal Plain (Fig. 28).

Landoltia is believed to have originated from South Asia or Australia (Landolt 1986) but is now widespread in warm-temperate to subtropical regions (Landolt 2000). It was first discovered from North America in Kansas City, Missouri, by Albert Saeger in 1934 (Ward 2011). *Landoltia* was possibly introduced via aquarium plant trade (Daubs 1965) and is becoming a noxious weed in the southeastern USA (Fig. 29a).

Landoltia was first described as a member of the genus *Lemna* but later placed into the genus *Spirodela*, along with other species that had more than one root per frond (Landolt 1986). Ward (2011) disputed the application of the basionym of *Lemma punctata*, believing that Thompson (1898) erroneously selected a collection of a different species (*Lemma oligorrhiza*) when transferring the species to his new combination, *Spirodela punctata*. Most modern authors disagree with Ward's conclusions and continue to recognize *Lemma punctata* as the correct basionym (Les & Crawford 1999; Wiersema 2015). Les and Crawford (1999) stated that is was "transitional between, but not a member of either *Lemna* or *Spirodela*" and placed *S. punctata* into a new genus, *Landoltia*. They also said that this monotypic genus "is very polymorphic in relation to size, pigmentation, number of roots, and veins." Since populations often contain individuals with only one root, it is best to examine a number of fronds in a population before making a determination. Daubs (1965) separated the two smaller species of *Spirodela* (now *Landoltia*) based on fronds being noticeably punctate with reddish-brown pigmented cells and having fewer roots.

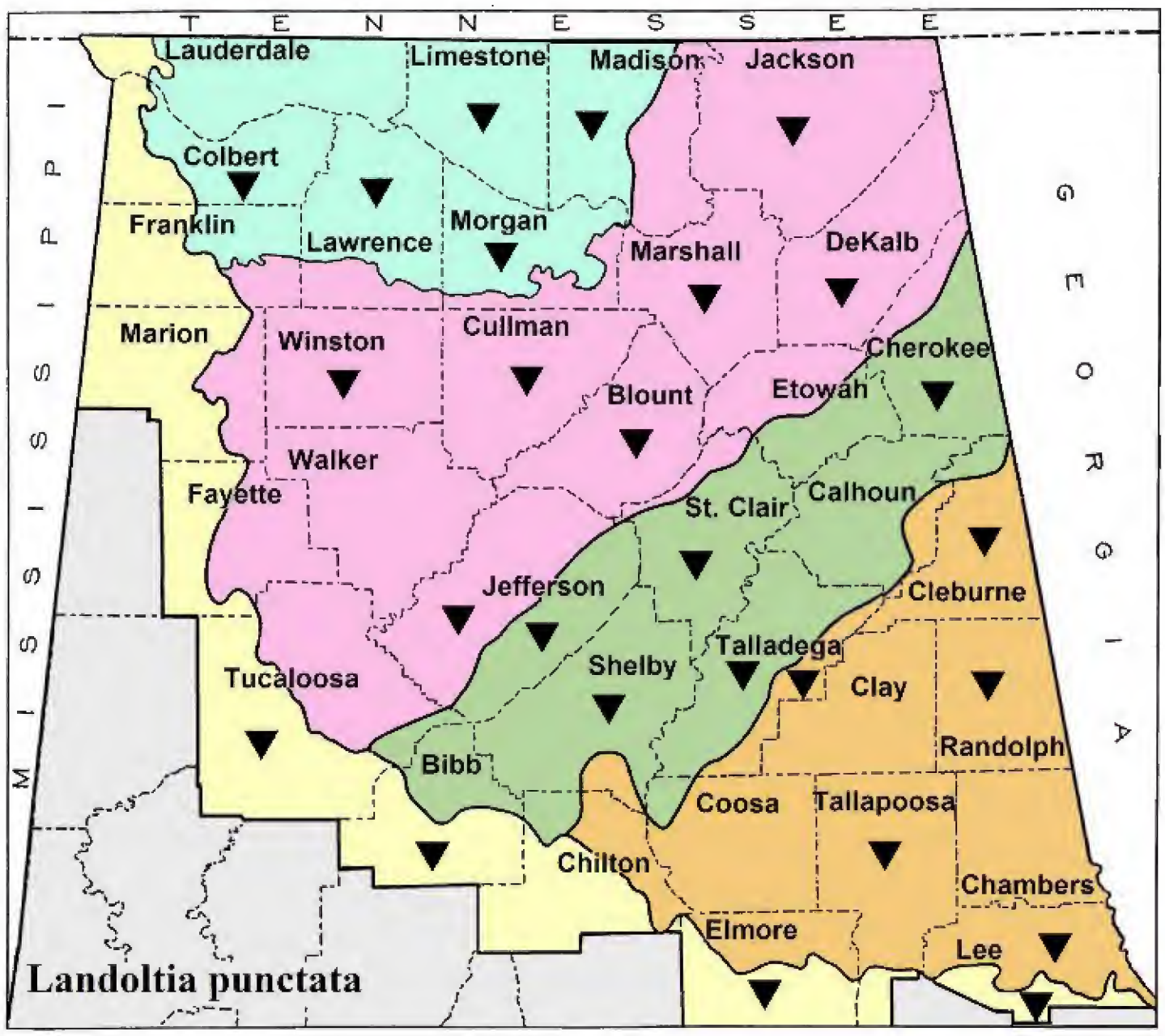


Figure 28. Distribution of *Landoltia punctata* in northern Alabama.

Although *Spirodela polyrrhiza* is similar to *Landoltia*, the latter has smaller, elongate-obovate fronds that lack a red spot (although fronds are sometimes dotted with reddish pigmentation). *Landoltia* also has fewer roots (Fig. 29b) than *Spirodela*, all of them perforating the scale-like leaflet. Moreover, turions are present in *S. polyrrhiza* but absent in *Landoltia* (Les & Crawford 1999). New fronds growing from the sides of the main fronds of *Landoltia* can mimic turions (Fig. 29c). These daughter fronds differ from turions by being the same color as the parent frond, remaining attached, and producing roots. True duckweed turions separate from parent fronds, sink, and later break dormancy after a period of cold temperatures (Kuehdorf et al. 2014).

(29a) Population on edge of pond. (29b) Frond roots. (29c) Daughter fronds similar in color.

Figure 29. *Landoltia punctata*. A. Cleburne Co., Alabama, 4 Aug 2019. B. Bankhead Lake, Jefferson Co. Alabama, 2 Jun 2018. C. Fronds from a pond in Cullman Co., Alabama, 27 Feb 2019. Photos: Dan Spaulding.

5. WOLFFIA Horkel ex Schleiden 1844

[Named for Johann F. Wolff, 1778–1806, German botanist who wrote about *Lemna*]

Wolffia is the smallest flowering plant in the world with fronds the size of a pinhead (Daubs 1965). All the duckweeds (*Landoltia, Lemna, Spirodela*, *Wolffia*, and *Wolffiella*) are used as food by wildlife, especially ducks, marsh birds, and shorebirds (Martin et al. 1951). Two species of *Wolffia* are known from Alabama and they sometimes grow intermixed.

1. Upper surface of frond with a distinct, single cone-shaped papule in the center; fronds often brown-punctate when dying, dead, or dried; cells inflated in lower portion of frond becoming progressively smaller and compact toward the upper surface; thus fronds are darker green in the top portion and lighter green or whitish in the lower section; all fronds floating no matter how crowded..... **1. Wolffia brasiliensis**
1. Upper surface of frond with a median row of smaller papules, but lacking a single nipple-like papule; fronds never brown-punctate; cells of frond all the same size, appearing uniformly green from the side; some fronds may occur under water in dense populations..... **2. Wolffia columbiana**

1. Wolffia brasiliensis Wedd. {of Brazil} — BRAZILIAN WATERMEAL (Fig. 30). [*Wolffia papulifera* C.H. Thomps.; *Wolffia punctata* Griseb.]

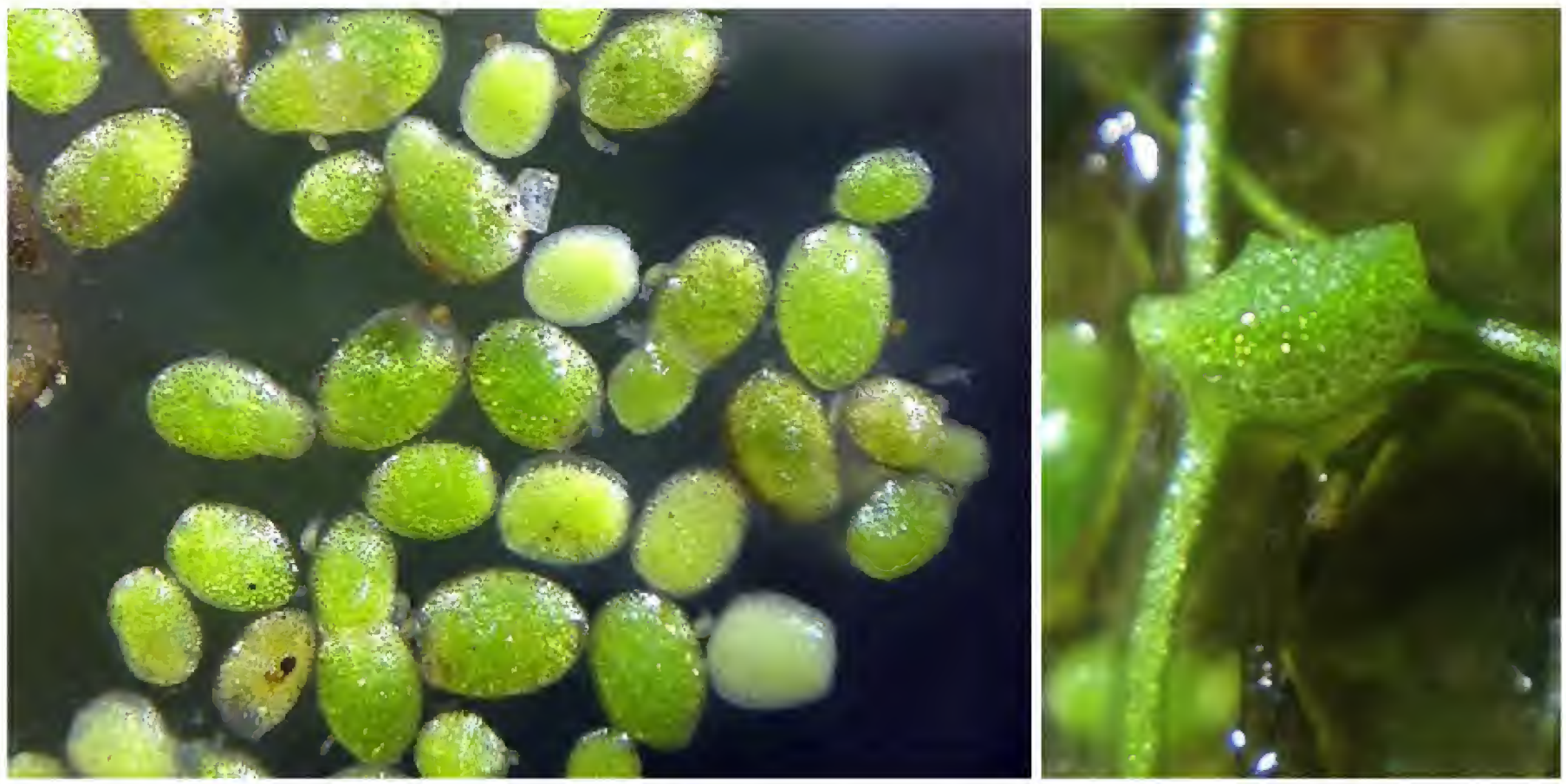


Figure 30. *Wolffia brasiliensis*, Snake Lake, Cleburne Co., Alabama, 8 Jun 2018. Photos: Dan Spaulding.

Floating aquatic, perennial herb. Still or very slow moving water of ponds, creeks, streams, impoundments, sloughs, swamps, and springs; rarely flowers and fruits in late spring–early fall (Landolt 2000); uncommon in the Highland Rim and Ridge & Valley; rare in the Cumberland Plateau and Piedmont; frequent in the Coastal Plain (Fig. 31). This species is native throughout the Americas. In the USA, it occurs mostly in eastern to midwestern states, and is disjunct on the west coast (Kartesz 2018).

Even though fronds of *Wolffia brasiliensis* are almost the size of a pinhead (Fig. 32a), populations often cover the entire water surface (Fig. 32b). Fronds are nutshell-like or boat-shaped (ellipsoid or broadly ovoid) and the upper surface is flat, except for a single, conical papule (nipple-like projection) in the center (Fig. 32c). Cells in the lower portion are inflated, becoming

progressively smaller and more compact toward the upper surface, which makes the frond appear darker at the top (Fig. 32c). These characters are detectable only under magnification and are easier to see in fresh specimens viewed from the side. Identification is also facilitated by brownish pigmented cells (dark dots) that appear in dead, dying, or dried fronds (Fig. 32d).

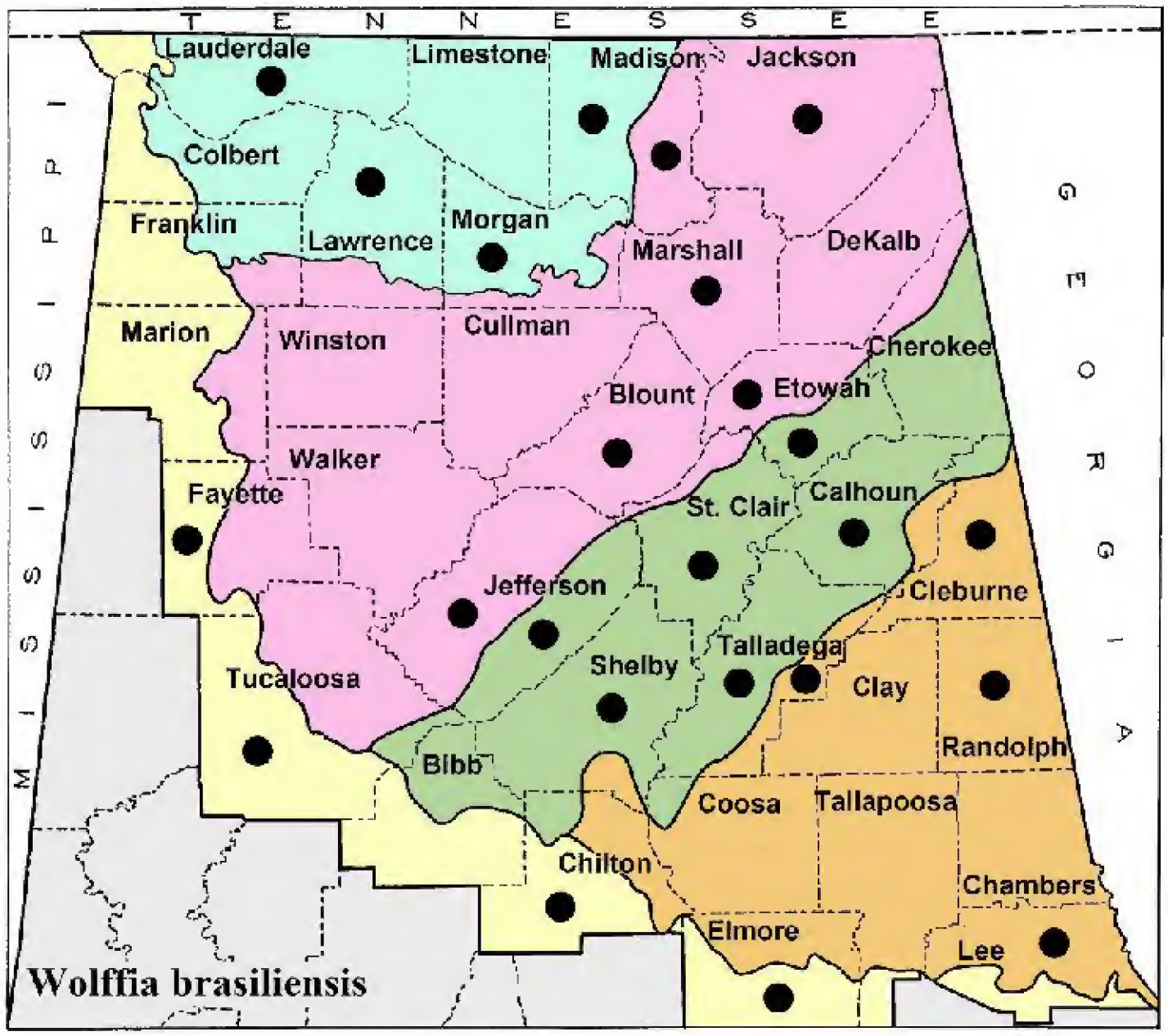
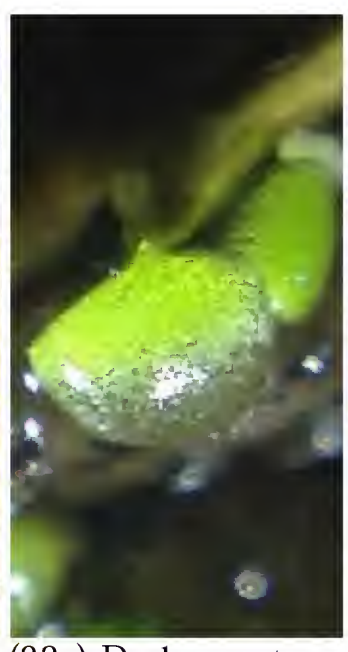


Figure 31. Distribution of *Wolffia brasiliensis* in northern Alabama.

(32a) Pinhead-sized fronds.

(32a) Population on pond.



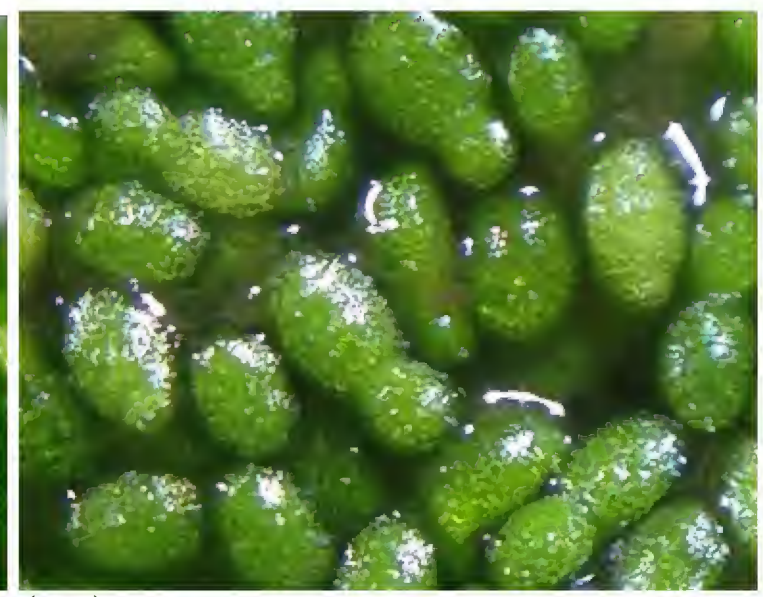
(32c) Darker on top.

(32d) Brown punctate frond.

Figure 32. *Wolffia brasiliensis*. A–B. Cleburne Co. Alabama, 20 Jun 2018. C. Lake Wedowee, Randolph Co., Alabama, 30 Jul 2018. D. Snake Lake, Cleburne Co., Alabama, 8 Jun 2018. Photos: Dan Spaulding.

2. Wolffia columbiana H. Karst. {of Colombia} — COLUMBIAN WATERMEAL (Fig. 33). [*Bruniera columbiana* (H. Karst.) Nieuwl.]

(33a) Frond (on *Landoltia*) lacking larger central papule.



(33b) Fronds floating and some submersed.

Figure 33. *Wolffia columbiana*. A. Marsh, Limestone Co., Alabama, 15 Jul 2018. B. Pond, Tallapoosa Co., Alabama, 10 Jul 2018. Photos: Dan Spaulding.

Floating aquatic, perennial herb. Still or very slow moving water of ponds, ditches, marshes, lakes, sloughs, oxbows, inlets, swamps, and rivers; very rarely flowers and fruits in summer–early fall (Landolt 2000); uncommon in the Highland Rim and Ridge & Valley; rare in the Cumberland Plateau and Piedmont; frequent in the Coastal Plain (Fig. 34). *Wolffia columbiana* is native to the Americas, from Canada south to Colombia and Venezuela (Daubs 1965).

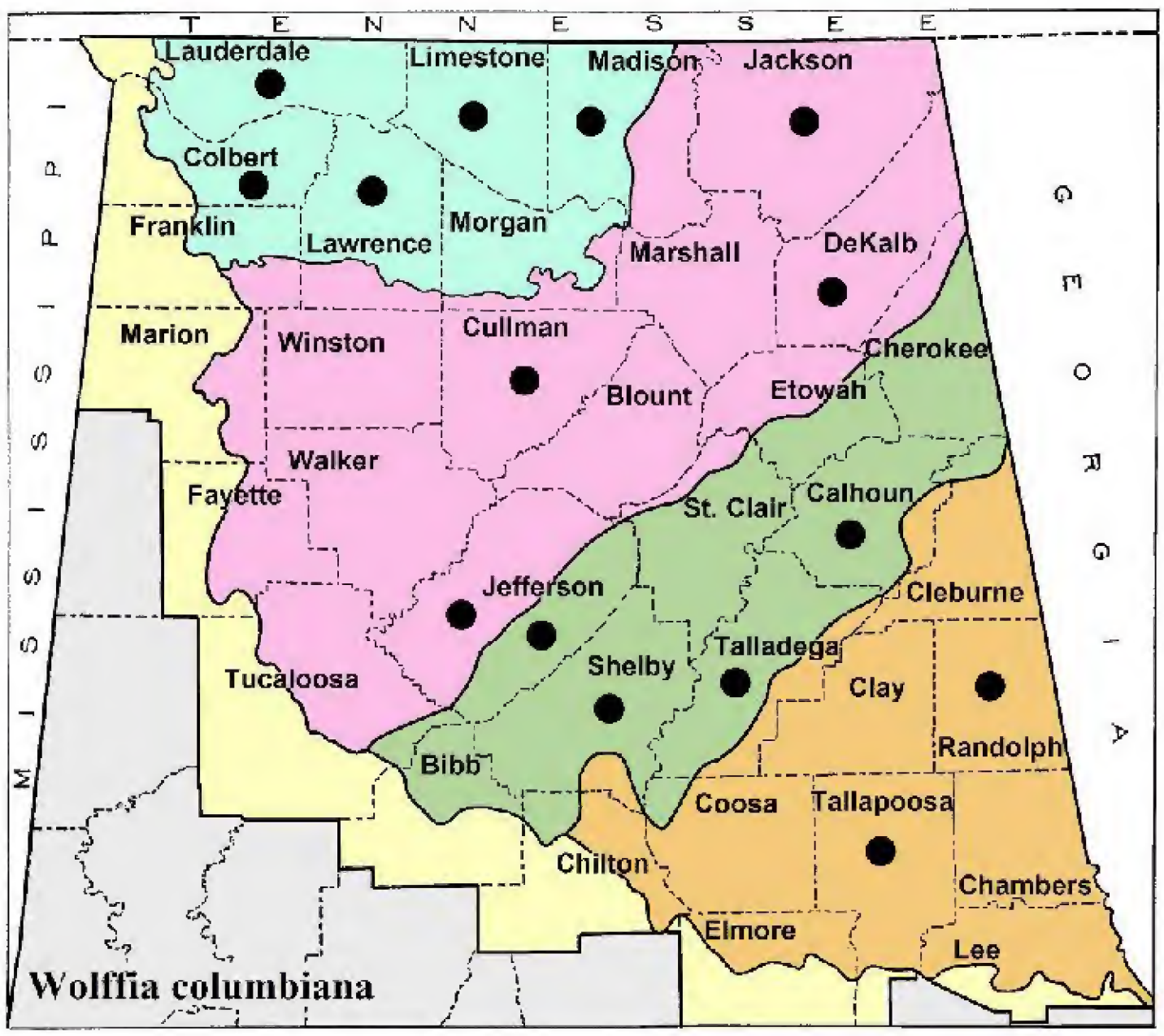


Figure 34. Distribution of *Wolffia columbiana* in northern Alabama.

Fronds of *Wolffia columbiana* are ovoid to globose and rounded (convex) on the upper surface. They typically have a median row of small papules, but lack a prominent, central papule (Fig. 33a). Fronds are never brown punctate (lack dots), and appear uniformly green from the side, since the cells are similar in size throughout. When crowded, individual fronds will often be forced under water (Fig. 33b), which is never the case in *W. brasiliensis*. Columbian Watermeal commonly occurs in mixed populations with other duckweed genera, such as *Landoltia* (Fig. 35).

Figure 35. *Wolffia brasiliensis* with *Landoltia punctata* on surface of a wastewater treatment pond in Wedowee, Randolph Co., Alabama, 13 Jun 2018. Photos: Dan Spaulding.

6. WOLFFIELLA Hegelmaier 1895

[Diminutive of *Wolffia*, named for Johann Friedrich Wolff, 1778–1806]

1. Wolffiella gladiata (Hegelm.) Hegelm. — MUD-MIDGETS; SWORD BOGMAT (Fig. 36).

Figure 36. *Wolffiella gladiata* at Summit Metro Parks in Triangle Lake Bog, Portage Co., Ohio, 23 May 2016. Photos: Rob Curtis.

Floating aquatic, perennial herb. In quiet waters of swamps, reservoirs, marshes, ponds, and sloughs; rarely flowering and fruiting in spring–fall (Landolt 2000); very rare in the Highland Rim and Cumberland Plateau (Fig. 37); infrequent in the Coastal Plain. This species is found primarily on the Coastal Plain from Massachusetts to east Texas, but scattered northward to southeast Oklahoma, west through the Ohio River Valley to Pennsylvania (Kartesz 2018).

Wolffiella is a monophyletic genus containing 10 species and is restricted to tropical to warm temperate areas of Africa and the Americas. This limited distribution is biogeographically unique

among the widespread temperate duckweed genera (Kimball et al. 2003). Allozyme and molecular phylogenetic studies suggest that the genus likely originated in Africa (Kimball et al. 2003; Crawford et al. 1997) with an early movement and subsequent radiation into the Americas (Kimball et al. 2003).

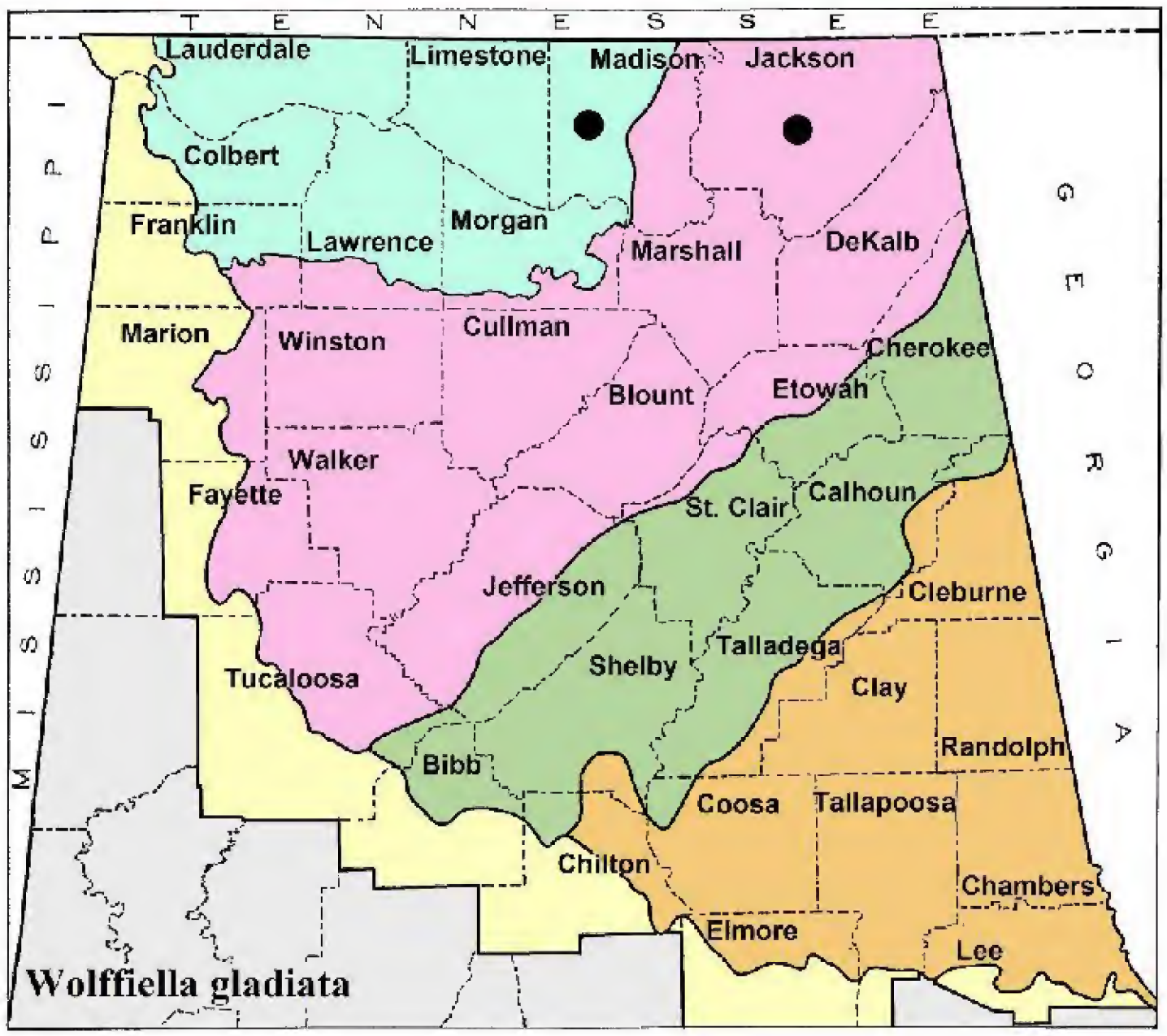


Figure 37. Distribution of *Wolffiella gladiata* in northern Alabama.

Wolffiella gladiata was recently discovered in northern Alabama by David Webb in Jackson County and later by Wayne Barger in Madison County. Like *Wolffia*, this genus lacks roots and veins, but differs by its flat, narrow, elongated fronds. When their sword-like fronds are connected, they can form a star-like structure (Fig. 38).

Figure 38. *Wolffiella gladiata*, Blackwell Swamp, Madison Co., Alabama, 15 Jun 2018. Photos: Wayne Barger.

7. PELTANDRA Rafinesque 1819

[Greek, *pelt* a small shield, and *andros*, male; referring to shape of tops of staminate flowers]

1. Peltandra virginica (L.) Schott {Virginian} — GREEN ARROW-ARUM; TUCKAHOE (Fig. 39). [*Peltandra luteospadix* Fern.; *Peltandra virginica* ssp. *luteospadix* (Fern.) W.H. & K.P. Blackw.]

Figure 39. *Peltandra virginica*, Autauga Co., Alabama, 27 May 2013. Photos: Brian Finzel.

Amphibious, perennial herb. Swamps, marshes, bogs, seeps, margins of lakes and ponds; flowers and fruits May–June; frequent throughout Alabama (Fig. 40). Native to eastern North America from southern Ontario and Quebec, south to Texas and Florida, and introduced in California, Oregon, and Washington (Kartesz 2018). Its original range has been expanding due to the dispersal of seeds by wildlife (Thompson 2000b).

Peltandra virginica generally has a green, succulent spathe, which occasionally has a whitish border. Its fruits are green to dark purple when ripe (Fig. 41a). A similar species, *P. sagittifolia* (Michx.) Morong [White Arrow-Arum], which is restricted to the southeastern Coastal Plain, differs by having a two-tone spathe that is solid white above and green at the base (Fig. 41b). Its fruits are red when ripe (Fig. 41c). Sterile material of these two species can be separated by their leaf venation. Leaves of both species have thick midveins, but the lateral veins of *P. sagittifolia* are all finely textured (Fig. 42a), while the lateral veins of *P. virginica* are thicker than the other veins (Fig. 42b).

Thompson (2000b) recognized only two species, *Peltandra virginica* and *P. sagittifolia*, stating that *P. virginica* is highly variable and that "different forms have been recognized taxonomically, both at the specific and infraspecific levels." Fernald (1948) named a third species *P. luteospadix* (Fig. 43), which he claimed differed from typical *P. virginica* because the upper portion of the spathe was flared and had a white border. The spathe of typical *P. virginica* is often tightly inrolled around the spadix and green throughout. Fernald's *P. luteospadix* is now considered to represent a form of *P. virginica*, which can be mistaken for *P. sagittifolia* due to its flaring white-margined spathe. Reports of *P. sagittifolia* from northern Alabama are most likely this form of *P. virginica*.

Blackwell and Blackwell (1974) reorganized the genus into a single species with two subspecies, *Peltandra virginica* subsp. *virginica* and *P. virginica* subsp. *luteospadix*. They

synonymized *P. sagittifolia* with subspecies *luteospadix*. Their taxonomic decision was based on the false assumption that "berries of all *Peltandreae* are in fact more or less green" and that spathes were "always somewhat greenish… In none we observed were the spathes entirely white… This is apparently an artifact of the drying process." The authors believed that *P. sagittifolia* was "a bit of fiction" and said "there is no such plant," which led them to an incorrect conclusion that "*Peltandra sagittifolia* was to be regarded as myth."

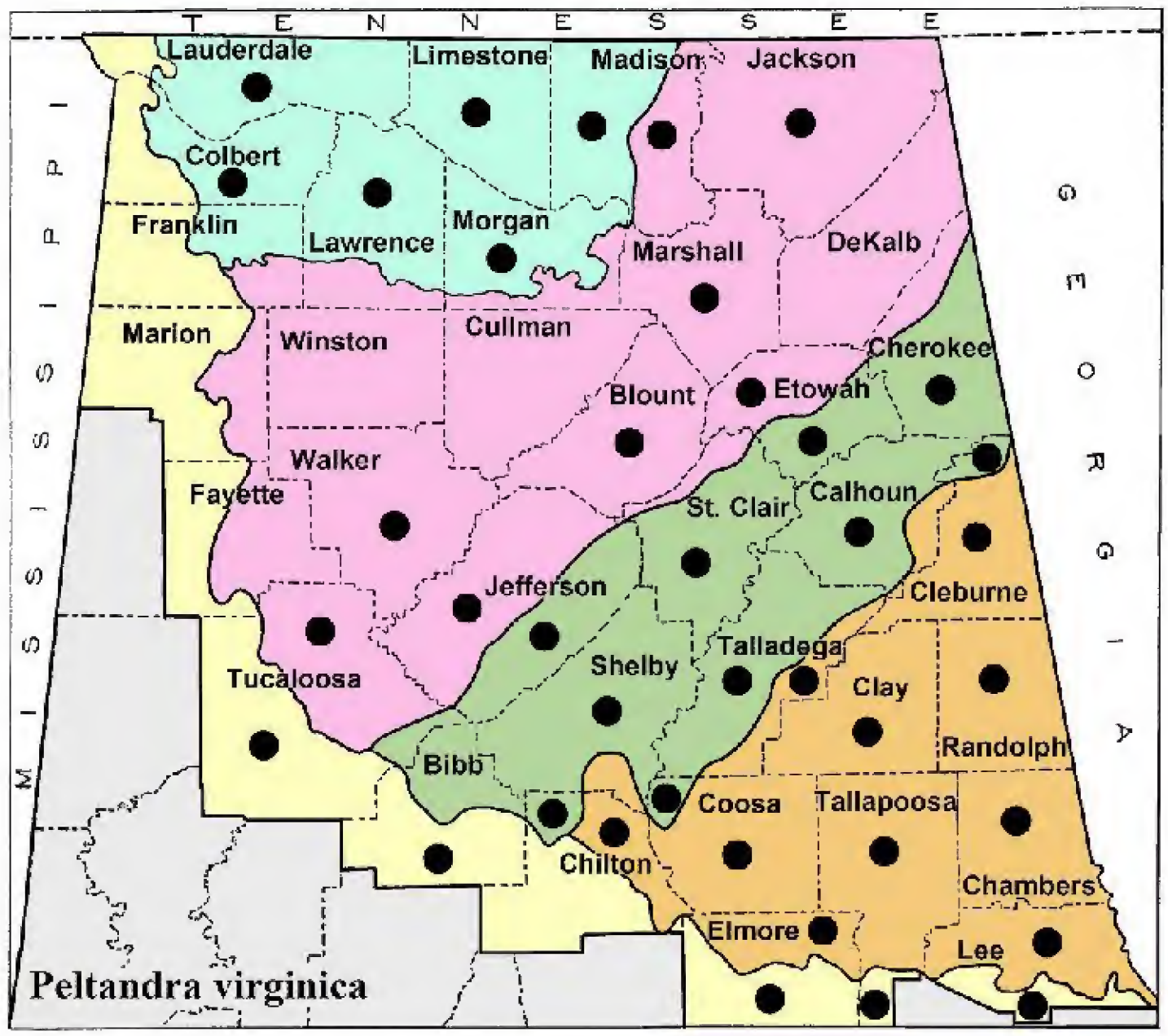


Figure 40. Distribution of *Peltandra virginica* in northern Alabama.

(41a) *Peltandra virginica* fruits.

(41b) *Peltandra sagittifolia* in flower.

(41c) *Peltandra sagittifolia* fruits.

Figure 41. A. Photo: Josef Bogner. <http://araceae.e-monocot.org/file/1271> B. Baldwin Co. Alabama, 19 Jun 2008. Photo: Wayne Barger. C. Perry Co. Mississippi, 14 Aug 2008. Photo: John Gwaltney. <http://www.southeasternflora.com>

(42a) *Peltandra sagittifolia* leaf.

(42b) *Peltandra virginica* leaf.

Figure 42. A. Perry Co. Mississippi, 14 Aug 2008. Photo: John Gwaltney. <http://www.southeasternflora.com>
B. Madison Co., Alabama, 8 Jun 2013. Photo: Brian Finzel.

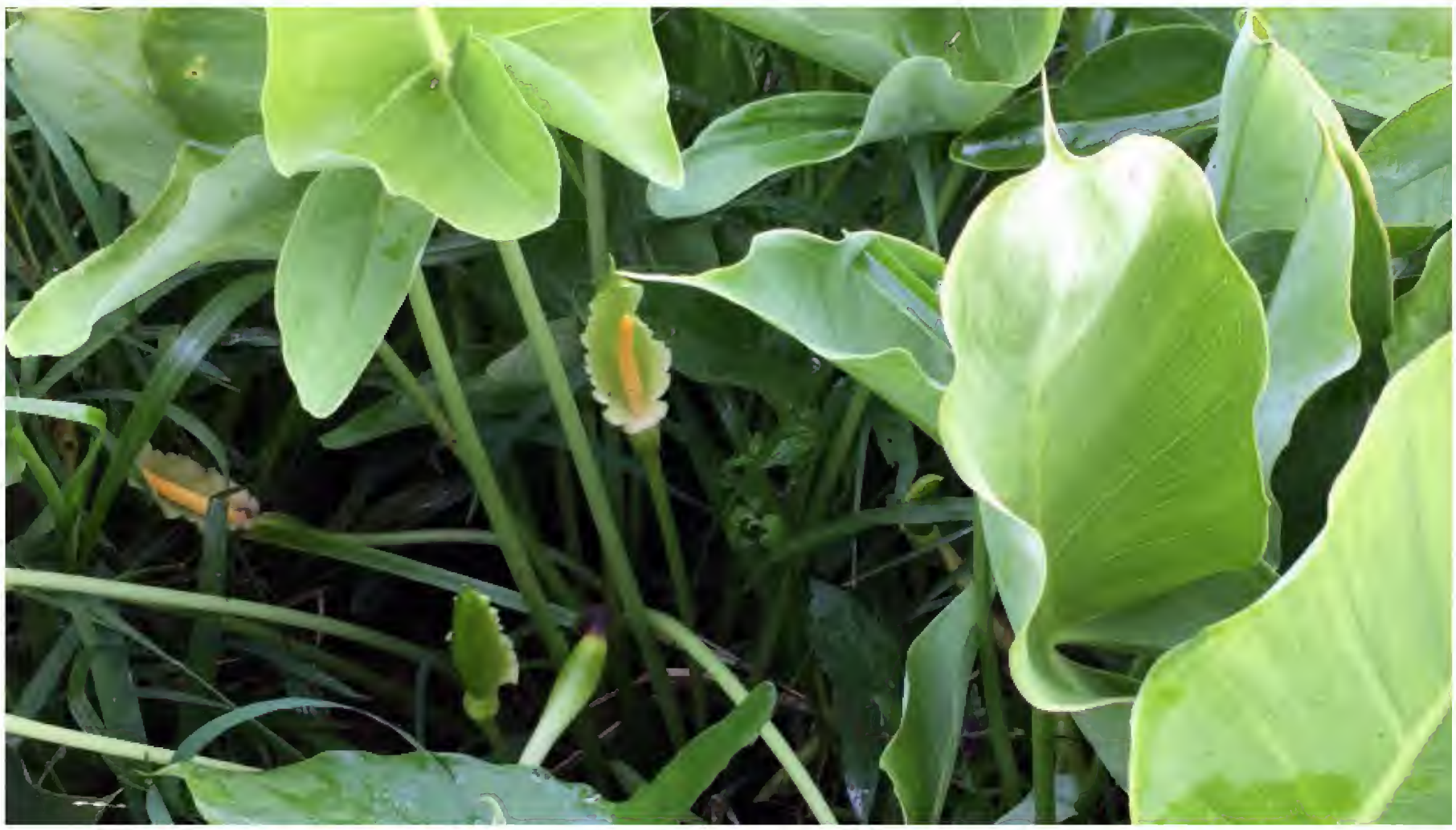


Figure 43. *Peltandra virginica* "*luteospadix*" along margin of lake in Delta, Clay Co., Alabama, 13 Jun 2018. Photo: Dan Spaulding.

Pollination studies of *Peltandra virginica* revealed that the unusual odor of the flowers attracts small flies (Patt et al. 1995). A species of chloropid fly (*Elachiptera formosa*) uses the inflorescence as a mating area and later as a food source for its larvae. The chloropid fly deposits its eggs on the spadix, enabling the emerging larvae to feed on the upper male portion, which is usually rotting when they hatch.

Coffey (1993) wrote that *Peltandra* was used historically as food by various Native American tribes of eastern North America. They ate the fruits, which allegedly sweeten after boiling, and utilized seeds from the berries to make bread. The starchy rhizomes have a potato-like flavor but need to be properly cooked prior to eating due to poisonous alkaloids. The vernacular name "tuckahoe" is actually an Algonquin Indian word, meaning edible roots.

8. PISTIA Linnaeus 1753

[Greek, *pistos*, liquid; referring to its aquatic habitat]

1. Pistia stratiotes L. {Greek for soldier; possibly referring to rows of leaves} — WATER-LETTUCE; WATER-CABBAGE; RIVER-LETTUCE; WATER-BONNET; SHELL-FLOWER (Fig. 44).

Figure 44. *Pistia stratiotes,* Lay Lake/Coosa River, Chilton Co., Alabama, 19 Jul 2018. Photo: Wayne Barger.

Floating aquatic, perennial herb with stolons. Slow or stagnant water along margins of rivers, lakes and inlets; very rarely flowers in late summer–early winter (Thompson 2000b); rare in the Cumberland Plateau, Ridge & Valley, Piedmont, and Coastal Plain (Fig. 45), but locally abundant. The center of origin of *Pistia stratiotes* is uncertain, but the species occurs worldwide mostly in tropical to subtropical regions (Adebayo et al. 2011). Some authors believe that *Pistia* may have originated in Africa since it is depicted in Ancient Egyptian hieroglyphs (Stoddard 1989). Center et al. (2002) suggested a South American origin because a large number of insects in Brazil and Argentina specialize on *Pistia*.

Water-Lettuce is the sole extant member of the ancient genus *Pistia* (Wilson 1960). It had long been thought to be in the evolutionary line to the duckweeds (Arber 1919). *Pistia stratiotes* flowers (Fig. 46a) are thought to be insect pollinated, but most plants in North America rarely set seed, possibly due to lack of pollinators (Haynes 1988). In northern Alabama, no flowers were observed in any populations. New plants are produced at the ends of stolons and spread by fragmentation (Fig. 46b). Water-Lettuce is a free-floating, stoloniferous aquatic with a rosette of velvety leaves and feathery roots that hang underneath (Fig. 46c). Its seeds are small and typically dispersed by water or occasionally transported on the feet of wading birds (Bown 2000).

Pistia was first observed in North America by John and William Bartram along the St. Johns River in Florida in the 18th Century (Stuckey & Les 1984). Based on the paleo-botanical, historical, and ecological evidence, Evans (2013) argued that *Pistia* is native to Florida. It is considered nonindigenous to all other states and was first documented from Alabama in 2002 (Thayer et al. 2018). New introductions, especially in the USA, are probably from the disposal or escape of

ornamental pond plants (Adebayo et al. 2011). Water-Lettuce listed as an extremely noxious weed because it clogs waterways and is perhaps one of the most invasive aquatic plants in the world (Dray & Center 2018). Kartesz (pers. comm. 2019) reported that from 6 individuals introduced into a private pond in Chapel Hill, North Carolina, produced about 1,600 plants in just over a 60-day period.

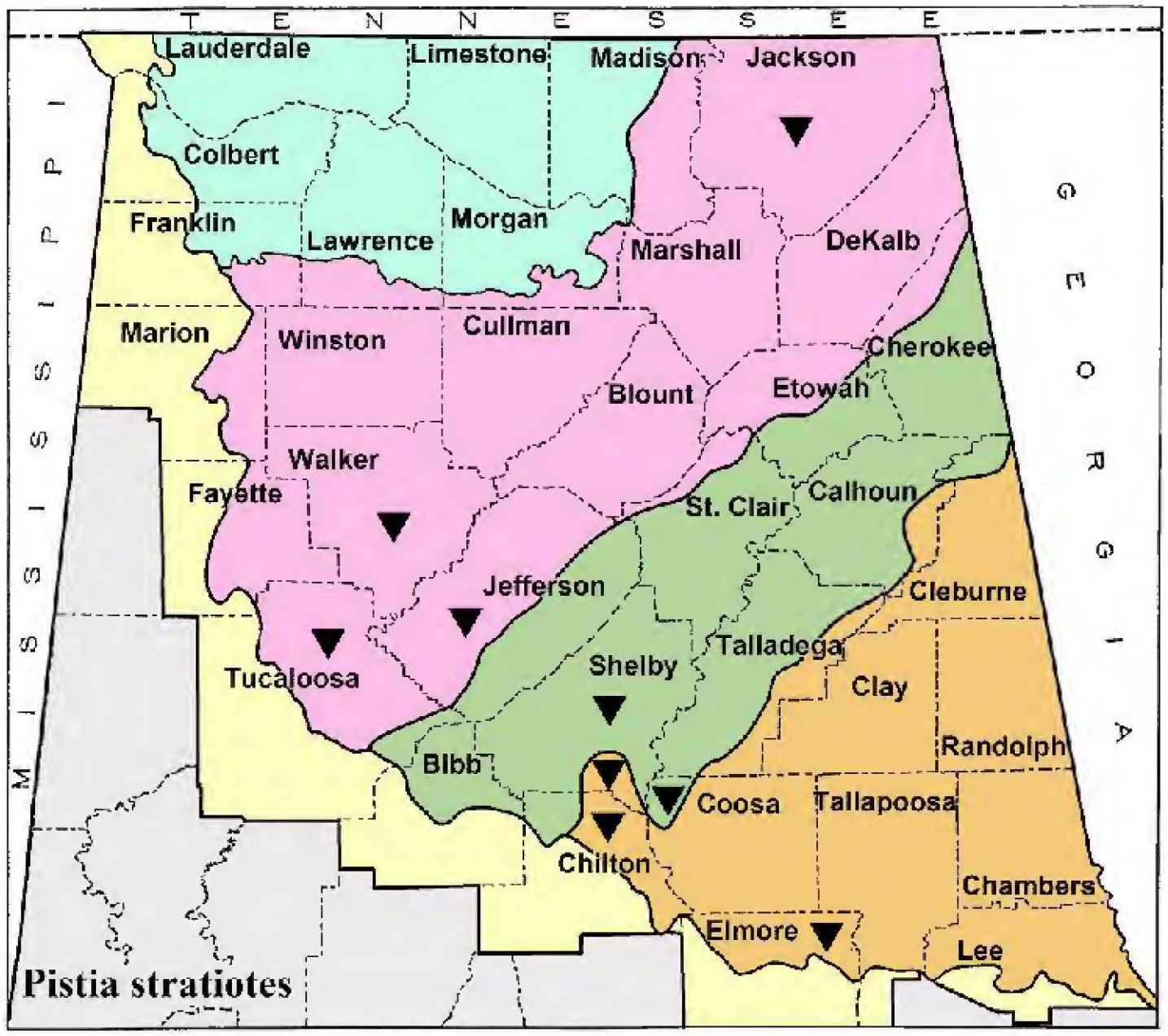


Figure 45. Distribution of *Pistia stratiotes* in northern Alabama.

(46a) *Pistia stratiotes* flowers resemble shells.

(46b) Dense population on lake.

(46c) Feathery roots.

Figure 46. *Pistia stratiotes*. A. Osaka Japan, 3 Nov 2005. Photo: Keisotyo. <https://commons.wikimedia.org> B. Lake Jordan Marina, Elmore Co., Alabama, 3 Sep 2018. Photo: Dan Spaulding. C. Maui, Hawaii. 20 Feb 2008. Photo: Forest & Kim Starr. <http://www.starrenvironmental.com>

9. COLOCASIA Schott 1832

[Greek name derived from an old Middle Eastern Arabic name of the plant, *colcus* or *culcas*]

1. Colocasia esculenta (L.) Schott {edible} — WILD TARO; COCO-YAM; ELEPHANT'S-EAR; DASHEEN; EDDO (Fig. 47). [*Colocasia antiquorum* Schott; *Colocasia esculenta* var. *antiquorum* (Schott) Hubb. & Rehder; *Colocasia esculenta* var. *aquatilis* Hassk.; *Colocasia esculenta* var. *nymphaeifolia* (Vent.) A.F. Hill]

Figure 47. *Colocasia esculenta* along banks of Choccolocco Creek, Talladega Co., Alabama, 21 Sep 2018. Photo: Dan Spaulding.

Amphibious, perennial herb with tuberous rhizomes. Along rivers, lakes, inlets, marshes, floodplains, canals, ditches, and wet disturbed areas; occasionally flowers and fruits June–October; uncommon in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Piedmont; frequent in the Coastal Plain (Fig. 48). Native to Asia and naturalized in the southeastern USA from North Carolina to Texas (Kartesz 2018), as well as Mexico, Central America, South America, Africa, Australia, Pacific Islands, and other tropical areas (Thompson 2000b).

Colocasia esculenta is widely cultivated in the tropics and subtropics for its starchy, edible tubers, making it one of the oldest crops in the world (Bown 2000). The tuber (corm), however, must be properly cooked prior to eating because it contains calcium oxalate crystals, which can severely irritate the tissues of the mouth (Wilson 1960). Taro is a staple food in the Pacific Islands, especially Hawaii, where they make poi (a fermented paste) from crushed, cooked corms (Thompson 2000b).

Because of Taro's long history of cultivation, many varieties and cultivars have been named. *Colocasia esculenta* is thought to have been introduced into the Caribbean and the southeastern USA by slaves who brought it from Africa (Thompson 2000b). Taro is widely planted in the Southeast and has escaped cultivation into areas beyond the southeastern Coastal Plain. It is locally abundant and can become an aggressive, invasive weed. Plants flower and fruit sporadically (Fig. 49a–d).

Colocasia mostly spreads vegetatively by stolons and rhizomes (Fig. 50a–b), forming large clonal colonies, especially along rivers and lakes. A key characteristic of *Colocasia* is its large, peltate leaves with a leaf stalk (petiole) that is attached on the underside of leaf blade (Fig. 50c).

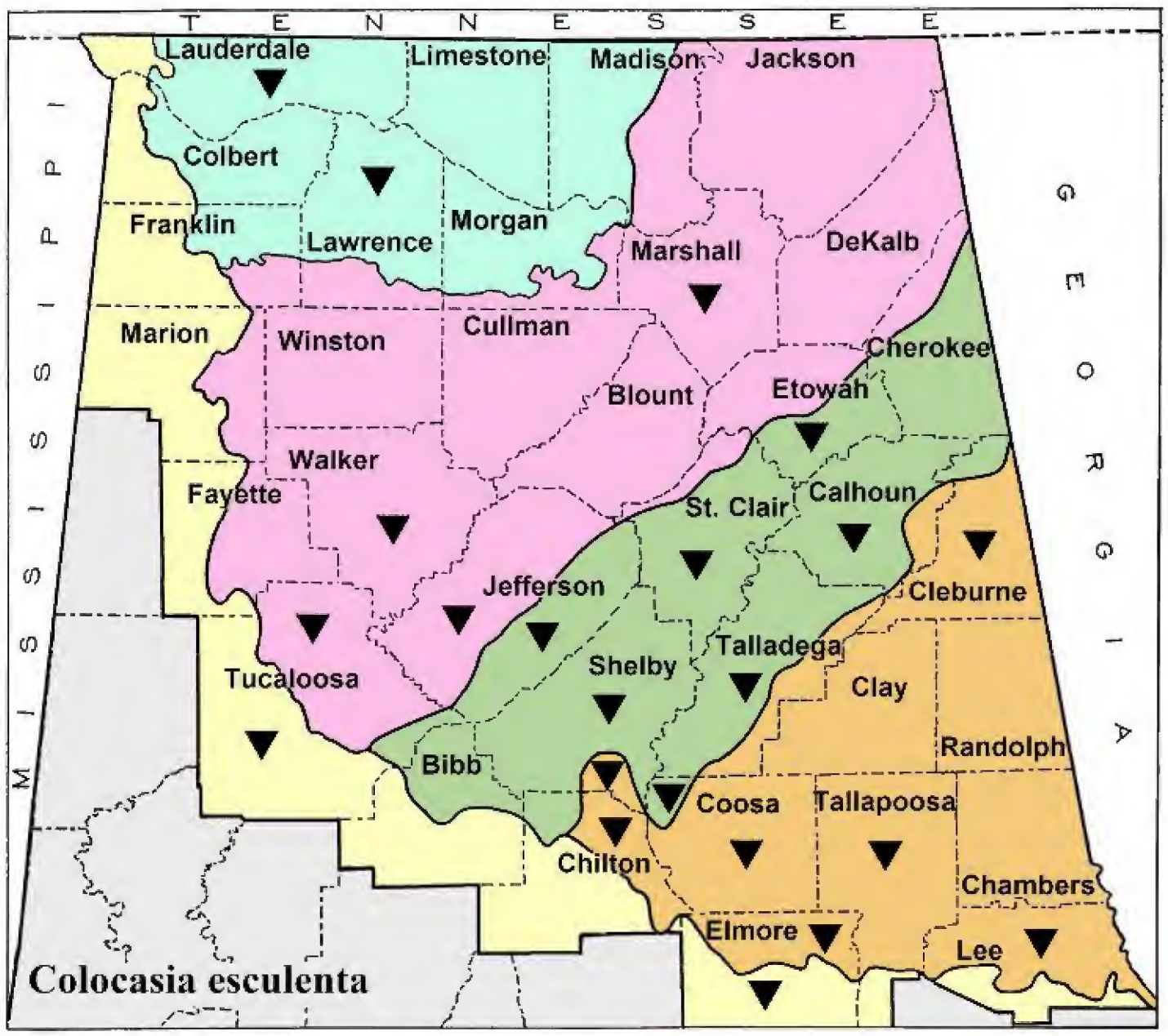
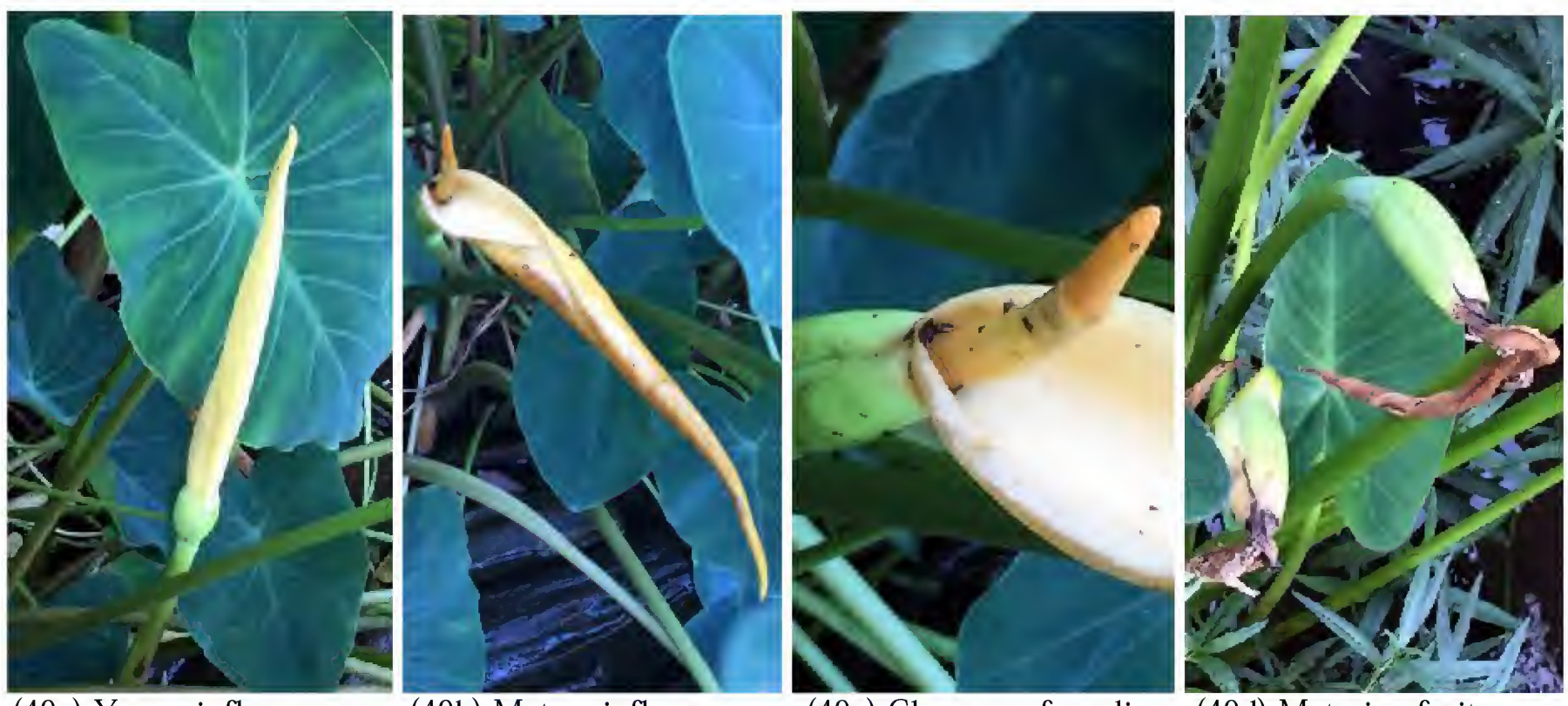


Figure 48. Distribution of *Colocasia esculenta* in northern Alabama.



(49a) Young inflorescence. (49b) Mature inflorescence. (49c) Close-up of spadix. (49d) Maturing fruits.

Figure 49. *Colocasia esculenta.* A–D. Margins of Black Warrior River, Jefferson Co., Alabama, 12 Oct 2018. D. Mulberry Fork of the Black Warrior River, Walker Co., Alabama, 22 Sep 2018. Photos: Dan Spaulding.

(50a) Base of plant with stolons. (50b) Plantlet at end of stolon. (50c) Peltate leaves.

Figure 50. *Colocasia esculenta*. A–C. Inlet into the Tennessee River, Lawrence Co., Alabama, 19 Aug 2018. C. Locust Fork of the Black Warrior River, Jefferson Co., Alabama, 2 Jun 2018. Photos: Dan Spaulding.

Serviss et al. (2000) listed three varieties of *Colocasia esculenta* (var. *antiquorum*, var. *aquatilis*, var. *nymphaeifolia*) occurring in the southeastern USA. The taxa are separated by lengths of rhizomes and size of tubers. Thompson (2000b) did not recognize any varieties and stated that "the species is extremely variable" and plants "are essentially all one morphologic form."

10. ARISAEMA Martius 1831

[Greek, *aris*, a kind of arum, and *haima*, blood; referring to red-spotted leaves of some species]

Taxa in the *Arisaema triphyllum* complex has been variously treated as species, subspecies, varieties, or forms. Small (1933) recognized them as species, Huttleston (1949, 1981) as subspecies, but Thompson (2000b) treated the complex as one highly variable species with multiple morphological forms. Weakley (2015) recognizes three distinct species and notes that the taxa "sometimes occur together in mixed populations with little sign of introgression or hybridization and seem to behave as biological species."

The distinguishing characteristics separating the members of the complex are often lost when specimens are pressed and dried, but they are easily identified in the field. *Arisaema dracontium* is distinct from the *A. triphyllum* complex but produces sterile hybrids with *A. stewardsonii* Britt., a species of the complex in the northeastern USA (Sanders & Burk 1992). *Arisaema* is considered poisonous because of needle-like, calcium oxalate crystals (concentrated in the corm) that can cause intense burning sensation if chewed (Gibbons et al. 1990).

1. Leaves pedately divided into (5-) 7–15 (21) unequal leaflets arranged on a semicircular axis (some divisions do not separate completely); spadix long-exserted from the spathe, 9–20 cm long, attenuate; summit of spathe hood with inrolled (involute) margins; fruit cluster conical to oblong ..... **1. Arisaema dracontium**
1. Leaves palmately divided into 3–5 subequal leaflets; spadix included within spathe, 3.5–8 cm long, club-shaped (clavate) or cylindrical and blunt; summit of spathe hood flat; fruit cluster ovoid or subglobose.

2. Leaves 5-foliolate, with all leaflets the same size (primary leaf has 5 leaflets, but secondary leaves sometimes 3-foliate); leaflets strongly glaucous beneath; spathe hood solid green; apex of spathe obtuse to abruptly pointed (apiculate); terminal portion of spadix (sterile appendix) curved or bent outward and often slender, but sometimes cylindrical..... **3. Arisaema quinatum**
2. Leaves primarily 3-foliolate (some plants occasionally have lobes on one or both lateral leaflets, but these are smaller than the primary leaflets); leaflets glaucous or green beneath; spathe hood solid green, solid purple or striped with white or purple; apex of hood long-acuminate or short-acute; terminal portion of spadix straight and cylindrical or club-shaped (clavate).

    3. Leaves glaucous (chalky-white) beneath at maturity; spathe hood up to 6 cm broad, green, green striped, or striped with purple (sometimes only on the underside of hood); spathe flange 4–9 mm wide; fruit cluster 2.5–6 cm long..... **4. Arisaema triphyllum**
    3. Leaves lustrous, light green beneath, not chalky-white; spathe hood up to 3.5 cm wide, solid green, green with white stripes, or occasionally uniformly purple (often just on the underside of hood), not purple-striped (although tube can be striped with purple); spathe flange 1–3 mm wide; fruit cluster 1.5–2.5 cm long..... **2. Arisaema pusillum**

1. Arisaema dracontium (L.) Schott {Greek name for a type of arum} — GREEN-DRAGON; DRAGON-ROOT; DRAGON-TAIL (Fig. 51). [*Muricauda dracontium* (L.) Small]

Figure 51. *Arisaema dracontium*, Tishomingo Co., Mississippi, 27 May 2007. Photo: Brian Finzel.

Perennial herb from corms. Rich woods, low woods, bottomland forests and floodplains; flowers April–June, fruits July–August; frequent in the Highland Rim, Cumberland Plateau, and Coastal Plain; uncommon in the Ridge & Valley and Piedmont (Fig. 52). Native to eastern North America from Canada south to eastern Mexico (Thompson 2000b).

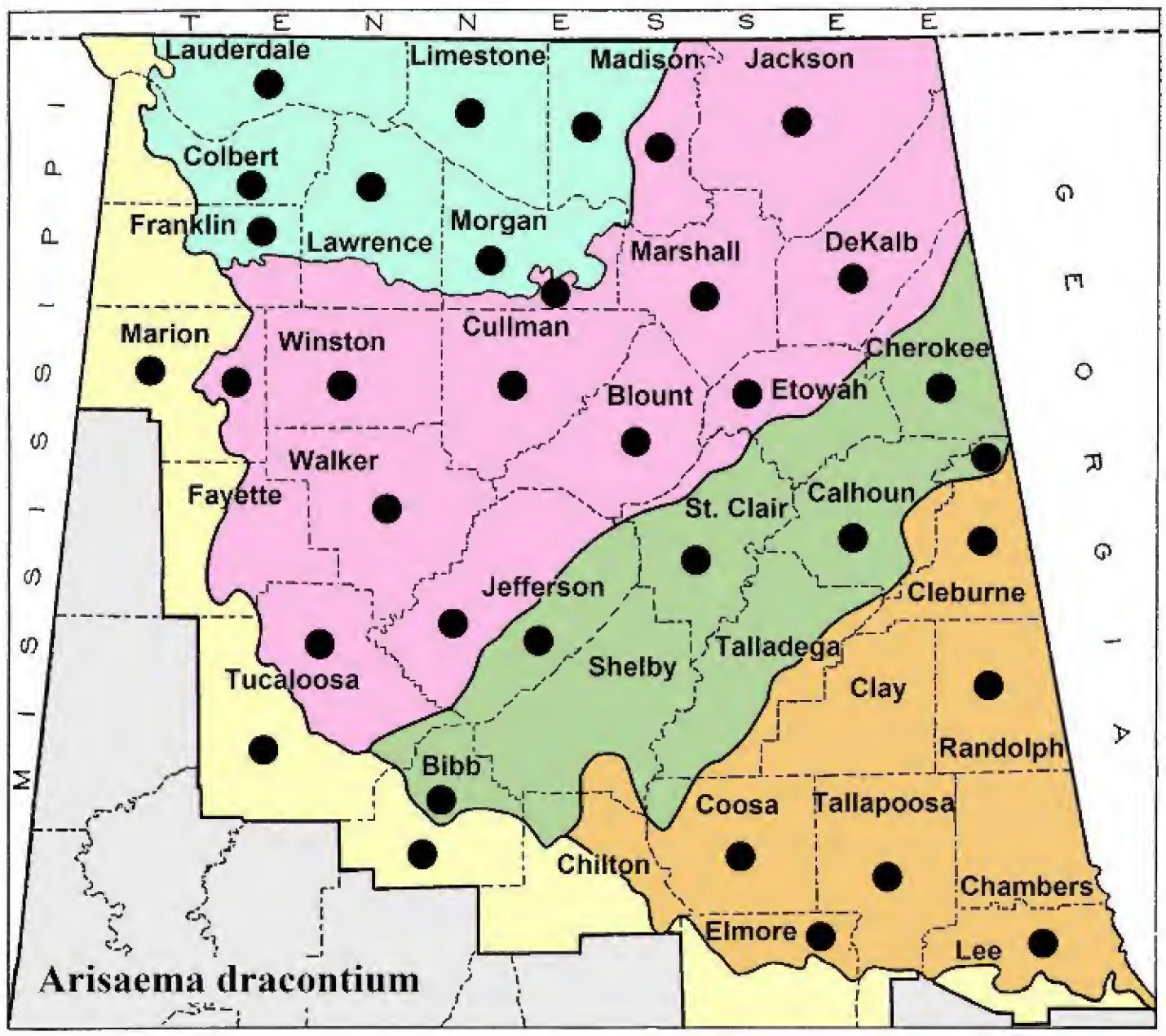


Figure 52. Distribution of *Arisaema dracontium* in northern Alabama.

(53a) Leaflet arrangement (plant with immature fruits). (53b) Inflorescence. (53c) Ripe fruits.

Figure 53. *Arisaema dracontium*. A. Colbert Co., Alabama, 16 Jun 2011. B. Madison Co., Alabama, 15 May 2012. C. Lawrence Co., Alabama, 27 Aug 2011. Photos: Brian Finzel.

Leaves and flowers of *Arisaema dracontium* are strikingly different from those of other species in the genus. Its leaflets are arranged on a semicircular axis, held out horizontally (Fig. 53a).

Its elongated spadix (Fig. 53b) possibly gave rise to the common names "dragon-flower" because it somewhat resembles a flickering lizard's tongue or tail (Shosteck 1974). In Florida, Ward (2012) recognized *A. dracontium* var. *macrospathum* (Benth.) Huttl. ex D.B. Ward, which has a flared blade-like spathe rather than a tightly inrolled spathe.

Clay (1993) stated that *Arisaema dracontium* is able to switch genders annually. Younger plants produce only male flowers, but as they mature, they become monoecious, producing both male and female flowers on the same plant. Green-Dragon's bright red berries resemble those of Jack-in-the-Pulpit, but occur in conical, rather than globose clusters (Fig. 53c).

The exotic Chinese Green Dragon, *Pinellia pedatisecta* Schott (Fig. 54), resembles our native species and it is not recommended for cultivation because it has the potential of becoming an invasive weed (Xu & Chang 2017). *Pinellia pedatisecta* differs by the following characteristics: the female portion of the spadix is fused (adnate) to the spathe, its berries are pale to greenish-white when ripe, and its fruits are single-seeded (Li & Bogner 2010).

Figure 54. *Pinellia pedatisecta,* St. Louis Co. Missouri, 31 Aug 2018. Photos: Adam Rembert.

2. Arisaema pusillum (Peck) Nash {very small} — SMALL-FLOWER JACK-IN-THE-PULPIT; PECK'S JACK-IN-THE-PULPIT (Fig. 55). [*Arisaema triphyllum* (L.) Schott ssp. *pusillum* (Peck) Huttl.; *Arisaema triphyllum* var. *pusillum* Peck]

Figure 55. *Arisaema pusillum*, Ebenezer Swamp, Shelby Co., Alabama, 22 Apr 2017. Photos: Brian Finzel.

Perennial herb from corms. Seeps, bogs, floodplains, and margins of swamps; flowers late March–May, fruits July–September; frequent throughout Alabama (Fig. 56). Native to the eastern USA from Connecticut and New York south to Florida and west to eastern Texas (Huddleston 1949).

Arisaema pusillum is similar to *A. triphyllum* in appearance. Both species usually have only three leaflets, but rarely one or two lateral leaflets produce smaller lobes (Fig. 57a). *Arisaema pusillum* has lateral leaflets that are only slightly asymmetrical (Fig. 57b); its leaflets are lustrous, light green beneath (Fig. 57c); spathe hood is green, green striped (Fig. 58a), or sometimes nearly solid purple on the underside (Fig. 58b); the flange (collar-like fold along spathe margin) is not prominent, only 1–3 mm wide; and its fruit cluster is small, up to 2.5 cm long (Fig. 58c–d). *Arisaema triphyllum* has lateral leaflets that are strongly asymmetrical and chalky white beneath; its spathe hood can be purple-striped but not blotched purple; its spathe has a conspicuous wider flange (up to 9 mm wide); and its fruit cluster is larger, usually greater than 2.5 cm long.

Arisaema pusillum is sometimes called Small Jack-in-the-Pulpit, but older individuals often become quite large, so this common name is a misnomer. The specific epithet likely refers to the spathes of *A. pusillum*, which are typically smaller than those of *A. triphyllum*. The senior author often refers to *A. pusillum* as "Swamp Jack" because it is more often found in wetter habitats than *A. triphyllum*.

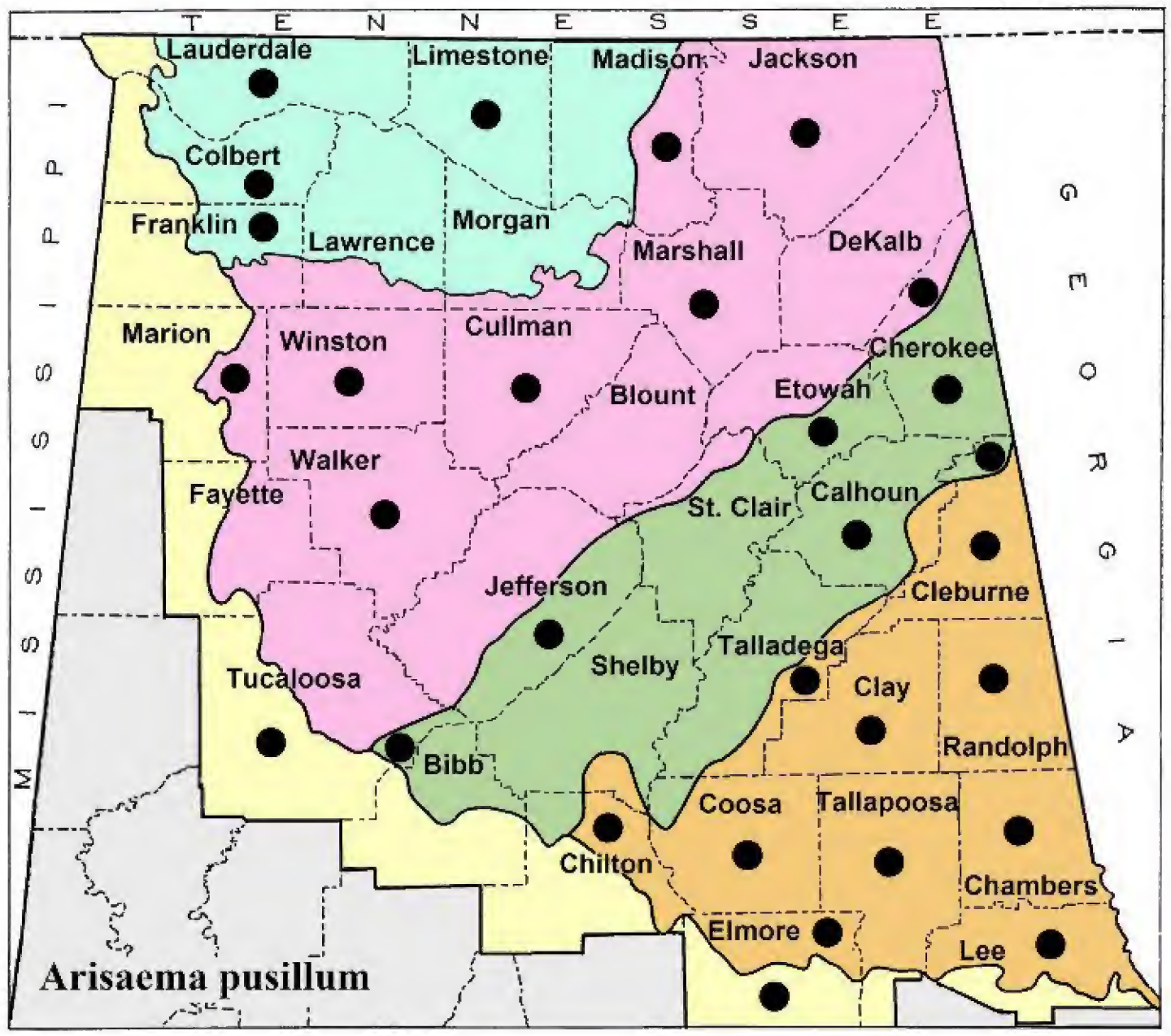
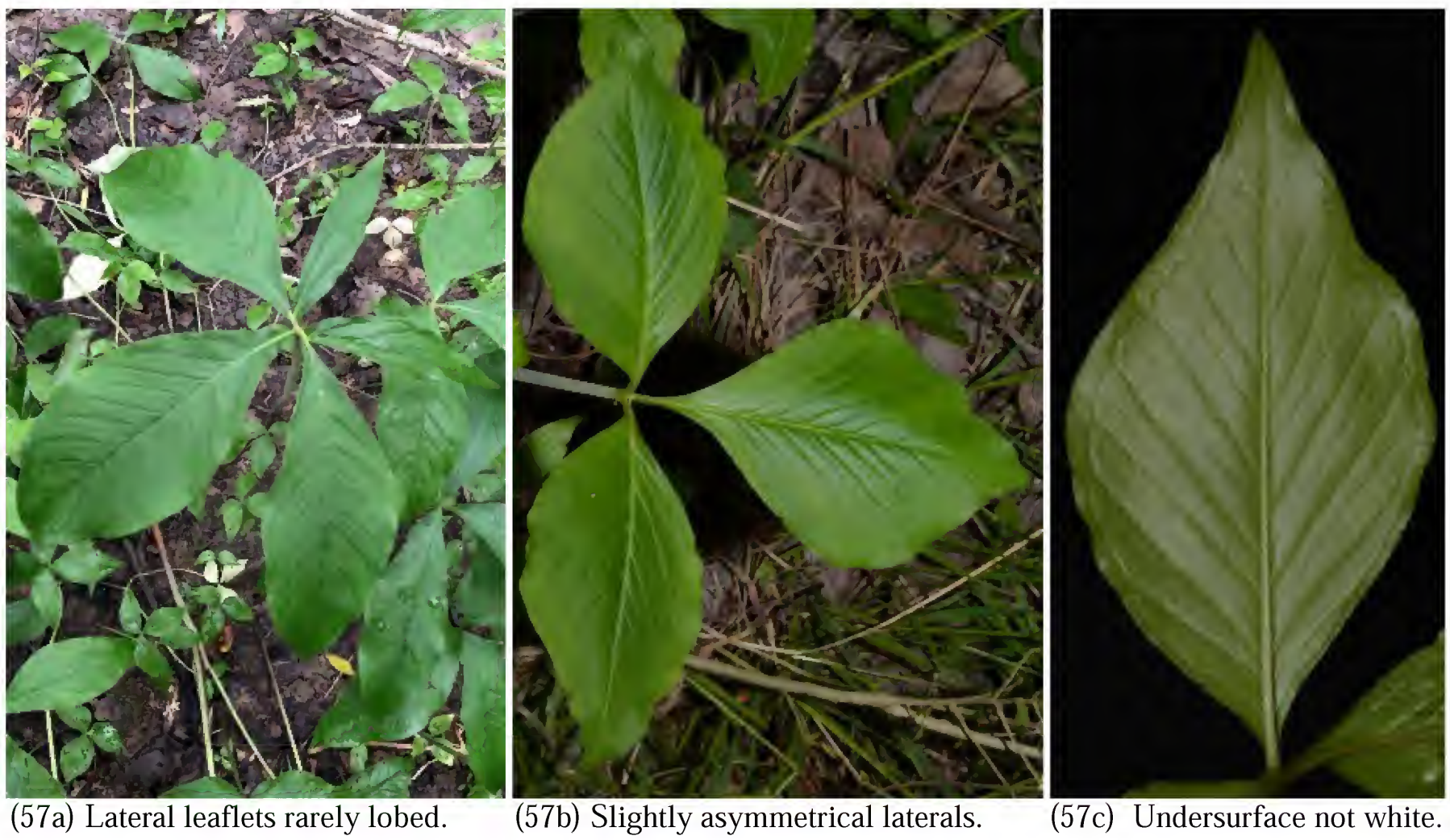


Figure 56. Distribution of *Arisaema pusillum* in northern Alabama.



(57a) Lateral leaflets rarely lobed. (57b) Slightly asymmetrical laterals. (57c) Undersurface not white.

Figure 57. *Arisaema pusillum*. A. Boggy woods, Etowah Co. Alabama, 18 Jun 2019. Photo: Dan Spaulding. C–B. Ebenezer Swamp, Shelby Co., Alabama, 7 May 2016. Photos: Brian Finzel.

(58a) Spathe often green striped. (58b) Solid purple hood below. (58c) Maturing fruits. (58d) Smaller fruit cluster.

Figure 58. *Arisaema pusillum*. A. Shelby Co., Alabama, 7 May 2016. Photo: Brian Finzel. B. Cleburne Co., Alabama, 12 May 2018. Photo: Dan Spaulding. C. Wake Co., North Carolina, 11 May 2018. Photo: Julie Tuttle. D. Randolph Co., Alabama 25 Aug 2019. Photo: Dan Spaulding. E. Randolph Co., Alabama 22 Sep 2018. Photo: Noah Yawn.

3. Arisaema quinatum (Nutt.) Schott {in fives} — FIVE-LEAF JACK-IN-THE-PULPIT; SOUTHERN JACK-IN-THE-PULPIT; PRESTER-JOHN; PREACHER-JOHN (Fig. 59). [*Arisaema triphyllum* (L.) Schott ssp. *quinatum* (Nutt.) Huttl.]

Figure 59. *Arisaema quinatum*, rich woods, Blount Co., Alabama, 20 Apr 2017. Photos: Brian Finzel.

Perennial herb from corms. Rich woods, mesic slopes, calcareous woods, and bottomlands; flowers late March–June, fruits July–September; uncommon in the Highland Rim and Coastal Plain; frequent in the Cumberland Plateau, Ridge & Valley, and Piedmont (Fig. 60). Endemic to the southeastern USA, ranging from North Carolina and Tennessee south to north Florida and eastern Texas (Godfrey & Wooten 1979).

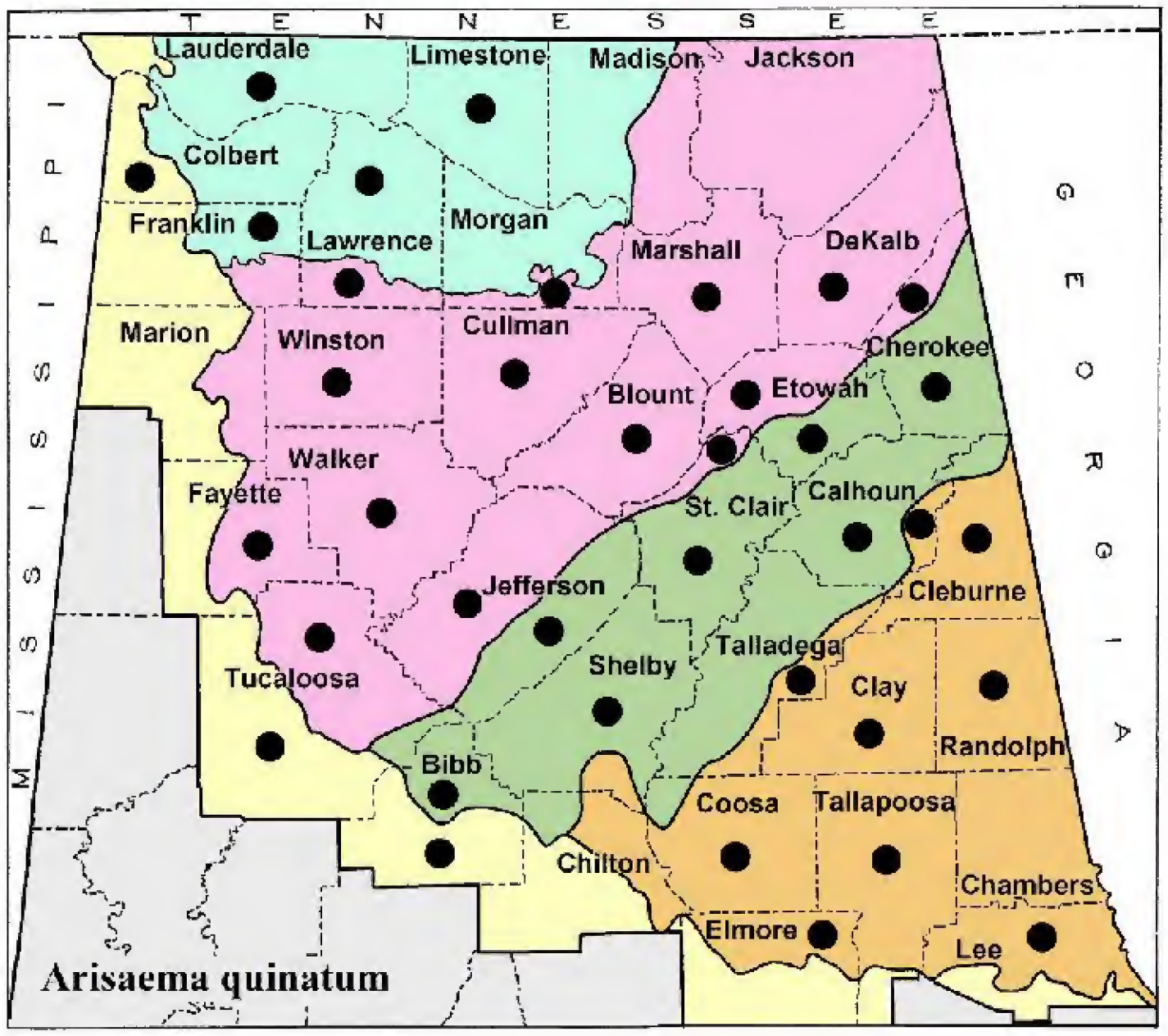


Figure 60. Distribution of *Arisaema quinatum* in northern Alabama.

(61a) Leaflets strongly glaucous underneath.

(61b) Spadix often bent.

Figure 61. *Arisaema quinatum*, hardwood forest, Fayette Co., Alabama, 15 Apr 2018. Photos: Dan Spaulding.

Arisaema quinatum differs from other members of the *A. triphyllum* complex by having five leaflets, rather than three (the secondary leaf can have three or five leaflets). Immature plants and seedlings are often trifoliate but are usually found growing next to mature plants. Like *A. triphyllum*, the leaves of *A. quinatum* are glaucous beneath (Fig. 61a), but its spadix is sometimes bent (Fig. 61b), somewhat resembling the spadix of *A. dracontium*, but much shorter.

4. Arisaema triphyllum (L.) Schott {three-leaved} — COMMON JACK-IN-THE-PULPIT; INDIAN-TURNIP; BROWN-DRAGON (Fig. 62). [*Arum triphyllum* L.; *Arisaema atrorubens* (Ait.) Blume]

Figure 62. *Arisaema triphyllum*, rich woods, Blount Co., Alabama, 19 Apr 2007. Photo: Brian Finzel.

Perennial herb from corms. Rich woods, mesic slopes, streambanks, low woods, and bottomland forests; flowers late March–June (peaks in April), fruits June–September; frequent throughout Alabama (Fig. 63). Native to eastern North America and Canada, from Nova Scotia to southeast Manitoba south to eastern Texas and northern Florida (Weakley 2015).

Arisaema triphyllum is the most common and widespread species in the genus (Treiber 1980). Its distinguishing characters are: trifoliate leaves that are chalky-white beneath; strongly asymmetrical lateral leaflets (Fig. 64); green to purple-striped spathes (Fig. 65a–b); and larger globose fruit clusters (Fig. 65c).

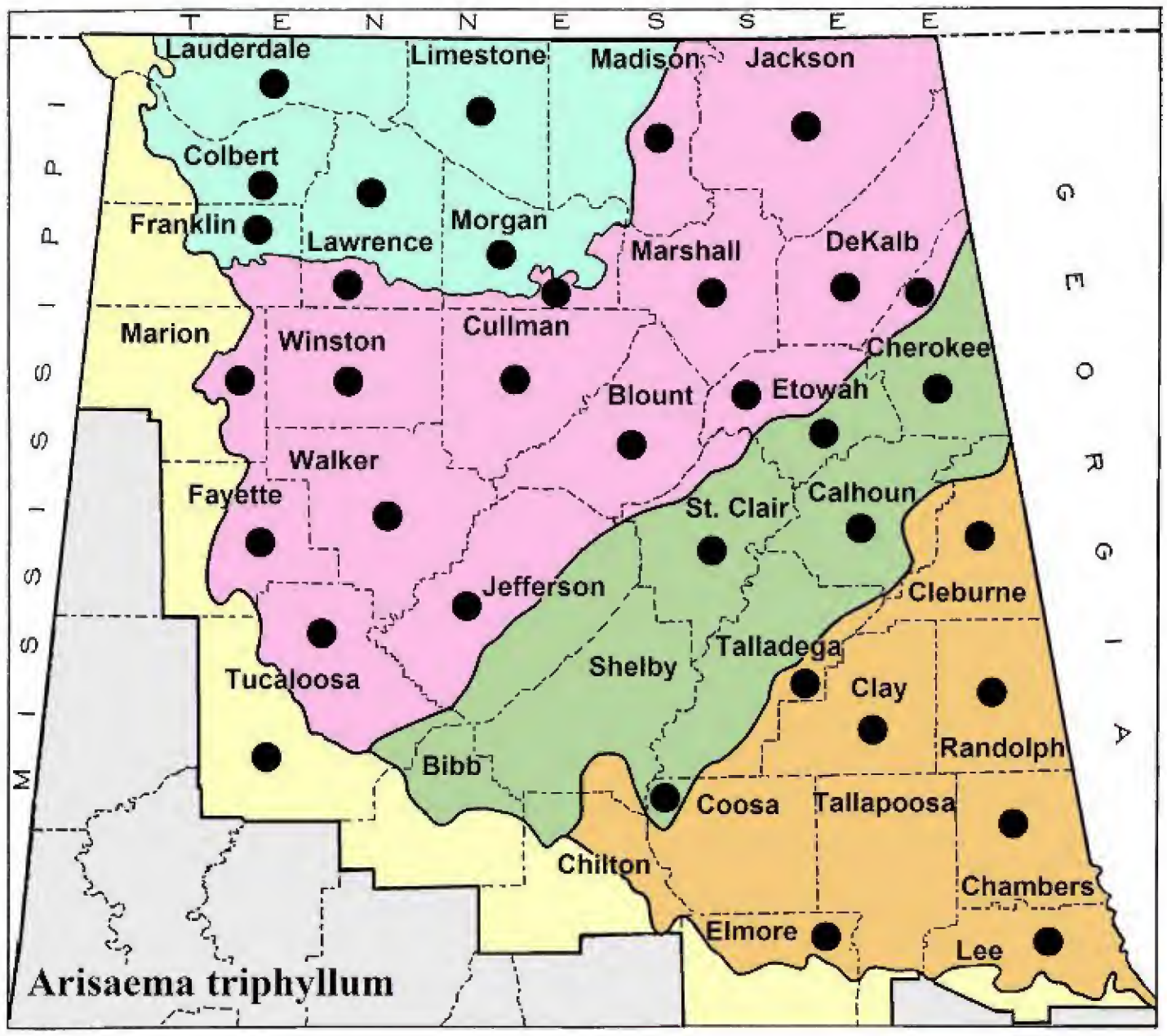


Figure 63. Distribution of *Arisaema triphyllum* in northern Alabama.

Figure 64. *Arisaema triphyllum* with strongly asymmetrical lateral leaflets that are chalky white beneath. Plant with immature globose fruit cluster (red when ripe). Fayette Co., Alabama, 2 Jun 2018. Photo: Dan Spaulding.

(65a) Green spathe. (65b) Purple-striped spathe. (65c) Immature fruit cluster with green berries.

Figure 65. *Arisaema triphyllum.* A. Cullman Co., Alabama, 2 Apr 2017. B. Sevier Co., Tennessee, 20 Apr 2015. C. Madison Co., Alabama, 15 Aug 2009. Photos: Brian Finzel.

Immature single-leaved plants are commonly found near mature plants, which appear to be vegetative off-shoots or seedlings. Camp (1932) noted that vegetative reproduction by "bud corms" is more common than reproduction by seeds. According to Rust (1980), Jack-in-the-Pulpit flowers are insect pollinated, primarily by thrips (Heterothripidae), springtails (Collembola), midges or fungus gnats (Mycetophilidae). In late summer and fall, plants produce a cluster of red berries, which are relished by Wild Turkey and Wood Thrush (Martin 1951).

Through maturation, Jack-in-the-Pulpit can change gender from male to female with varying degrees of bisexuality. In the first few years of life, plants are non-flowering but later produce male (staminate) flowers. Over time they develop female (pistillate) flowers at the base of the spadix, just below the male flowers. This hermaphroditic or monoecious stage usually lasts for several years, but at maturity, it transitions to being female (Camp 1932). However, if environmental conditions are poor or an individual expends too much energy producing fruit, it can revert back to a male or even become asexual again (Bown 2000). Historically, it has been thought that plants with green hoods were males and those with purple, females (Dana 1899), but there is no objective basis to this claim.

Jack-in-the-Pulpit gets its fanciful common name from the spadix appearing to represent a "preacher Jack" standing and surrounded by his pulpit with a sounding board, the spathe (Shosteck 1974). The whole plant, especially the corm, contains calcium oxalate crystals, which can cause a burning sensation if eaten raw. The colloquial name "memory-root" relates to a schoolboy trick of tempting others to bite into the tuber (Dana 1899). The name "Indian-Turnip" was derived from Native Americans use of the corms as food, but only after being properly prepared (Martin 1989). The peppery, tuberous root, as well as cooked berries, were important foods of Indians and early settlers (Coffey 1993).

11. ARUM Linnaeus 1753

[Latinized form of the Greek, *aron*, old name for these plants]

1. Arum italicum P. Mill. {Italian} — LORDS-AND-LADIES; ITALIAN ARUM; CUCKOO'S-PINT; ITALIAN-LILY (Fig. 66).

Figure 66. *Arum italicum*, disturbed woods, Calhoun Co., Alabama, 25 Apr 2018. Photos: Dan Spaulding.

Perennial herb with tubers. Suburban woodlands; flowers April–May, fruits July–September; very rare in the Ridge & Valley (Fig. 67). Native to Western Europe and North Africa around the Mediterranean region, where it inhabits woodlands and hedgerows (Tutin et al. 1980). *Arum italicum* is naturalizing from horticultural plantings in eastern and western coastal states of the USA (Kartesz 2018).

Arum italicum can spread quickly by tubers (Fig. 68a) and has the potential of becoming an invasive species (Randall 2001). Only the typical subspecies has been found to escape cultivation in the USA. The plant can be easily distinguished by the conspicuous whitish veins on its arrow-shaped leaves (Tutin et al. 1980). Scot Duncan, of Birmingham-Southern College, was the first to discover this species in Alabama in a disturbed forest on campus.

Lords-and-Ladies blooms in spring producing inflorescences of small, white monoecious (male and female) flowers borne at the base of a finger-like, green to greenish spadix. The spadix is surrounded by a green to greenish-white spathe (sheath-like bract). The flowers emit a foul, dung-like odor that attracts pollinators, such as dung beetles and flies (Linz et al. 2010). Following pollination, the spathe withers, leaving only a stalk of green berries, which turn bright orange-red at maturity (Fig. 68b). The glossy, variegated leaves also die back after flowering, but emerge in autumn and remain evergreen through winters in Alabama (Fig. 68c).

Like many plants within the Araceae, *Arum italicum* is toxic because of the needle-like calcium oxalate crystals (raphides), which cause intense burning when ingested (Bown 2000). Despite its toxicity, *Arum* has been used for food and medicinal purposes for centuries, especially as a treatment for warts and hemorrhoids (Azab 2017).

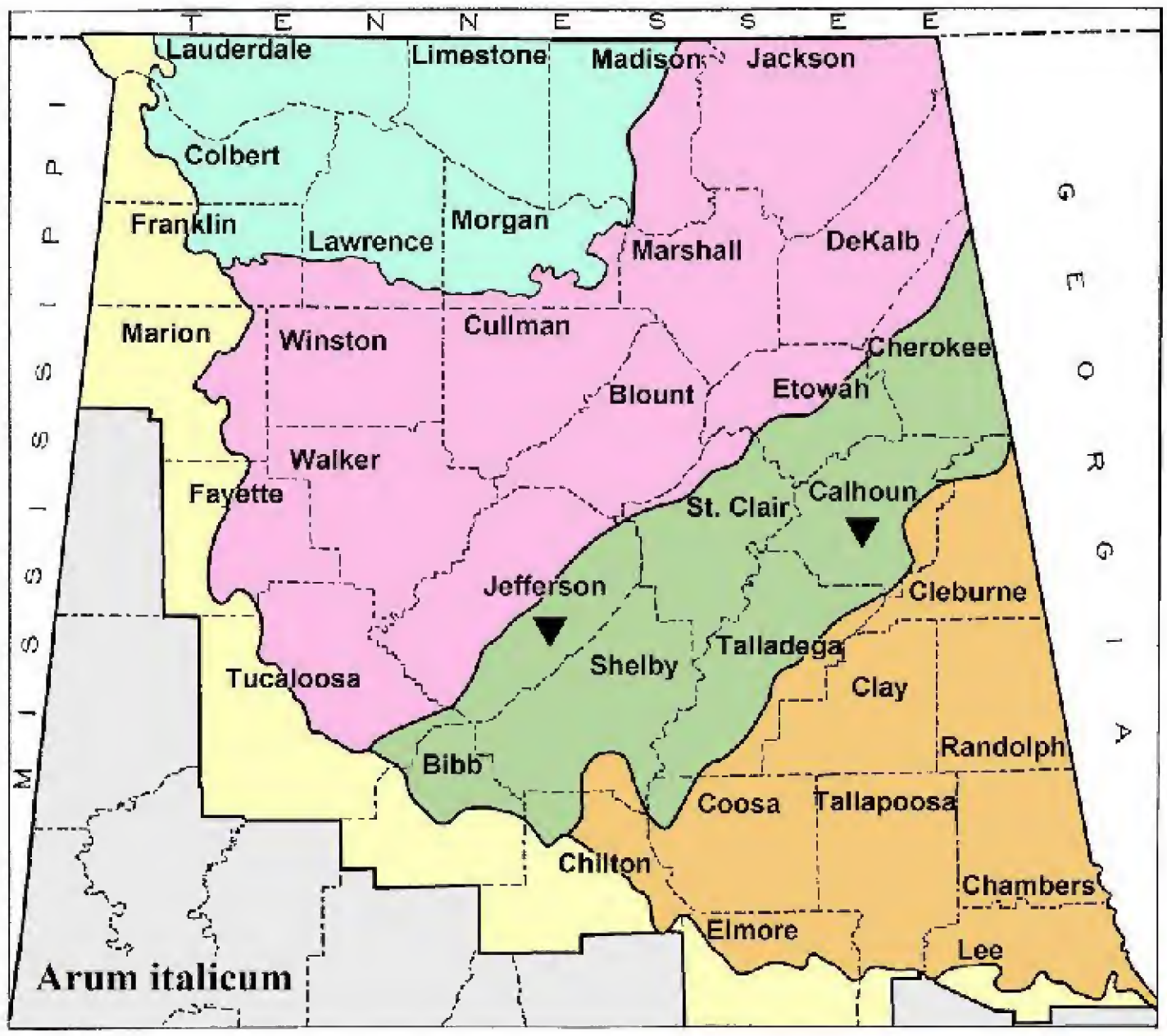


Figure 67. Distribution of *Arum italicum* in northern Alabama.

(68a) Tubers. (68b) Ripe fruits. (68c) Leaves in winter (coldest night).

Figure 68. *Arum italicum* in disturbed woods. A. Calhoun Co., Alabama, 30 Jan 2019. B. Calhoun Co., Alabama, 12 Jul 2018. C. Calhoun Co., Alabama, 30 Jan 2019. Photos: Dan Spaulding.

FAMILY 3. TOFIELDIACEAE (False-Asphodel Family)

Historically, members of this family were placed within the Liliaceae (Cronquist 1981; Utech 2002), but it is now shown to represent the most basal lineage within the order Alismatales and this family does not belong in the Liliales (Luo 2016). Tofieldiaceae consists of four genera: *Harperocallis*, *Pleea*, *Tofieldia*, and *Triantha*. Zomlefer (1997) included the last three genera within a broadly circumscribed *Tofieldia*, but Packer (2002) recognized them as distinct. Only two species, *Triantha racemosa* (Walt.) Small and *Pleea tenuifolia* Michx. [Rush-Featherling] are known from Alabama. *Pleea* is endemic to the southeastern Coastal Plain and differs from other genera within the family by its larger bracts and flowers. *Triantha* is distinguished from *Tofieldia* by its glandular-pubescent scapes with flowers in clusters of 2 or more (versus glabrous scapes with solitary flowers).

1. TRIANTHA (Nuttall) Baker 1879

[Greek, *tri*, three, and *anthos*, flower; in reference to flowers often clustered in threes]

1. Triantha racemosa (Walt.) Small {racemose} — SOUTHERN BOG-ASPHODEL; COASTAL-PLAIN BOG-ASPHODEL; COASTAL FALSE ASPHODEL; WOOD-FEATHERLING (Fig. 69). [*Tofieldia racemosa* (Walt.) B.S.P.]

Figure 69. *Triantha racemosa*, bog in Cherokee Co., Alabama, 30 Jun 2018. Photos: Brian Finzel.

Perennial herb with short rhizomes. Bogs, seepage slopes, and wet pine savannas; flowers June–August, fruits August–October; very rare in the Ridge & Valley and Piedmont; rare in the upper Coastal Plain, but frequent in the lower portions (Fig. 70). Chiefly found on the Coastal Plain from New Jersey south to northern Florida, west to east Texas. It is disjunct further inland in Maryland, Virginia, Georgia, Alabama, and central Tennessee (Kartesz 2018).

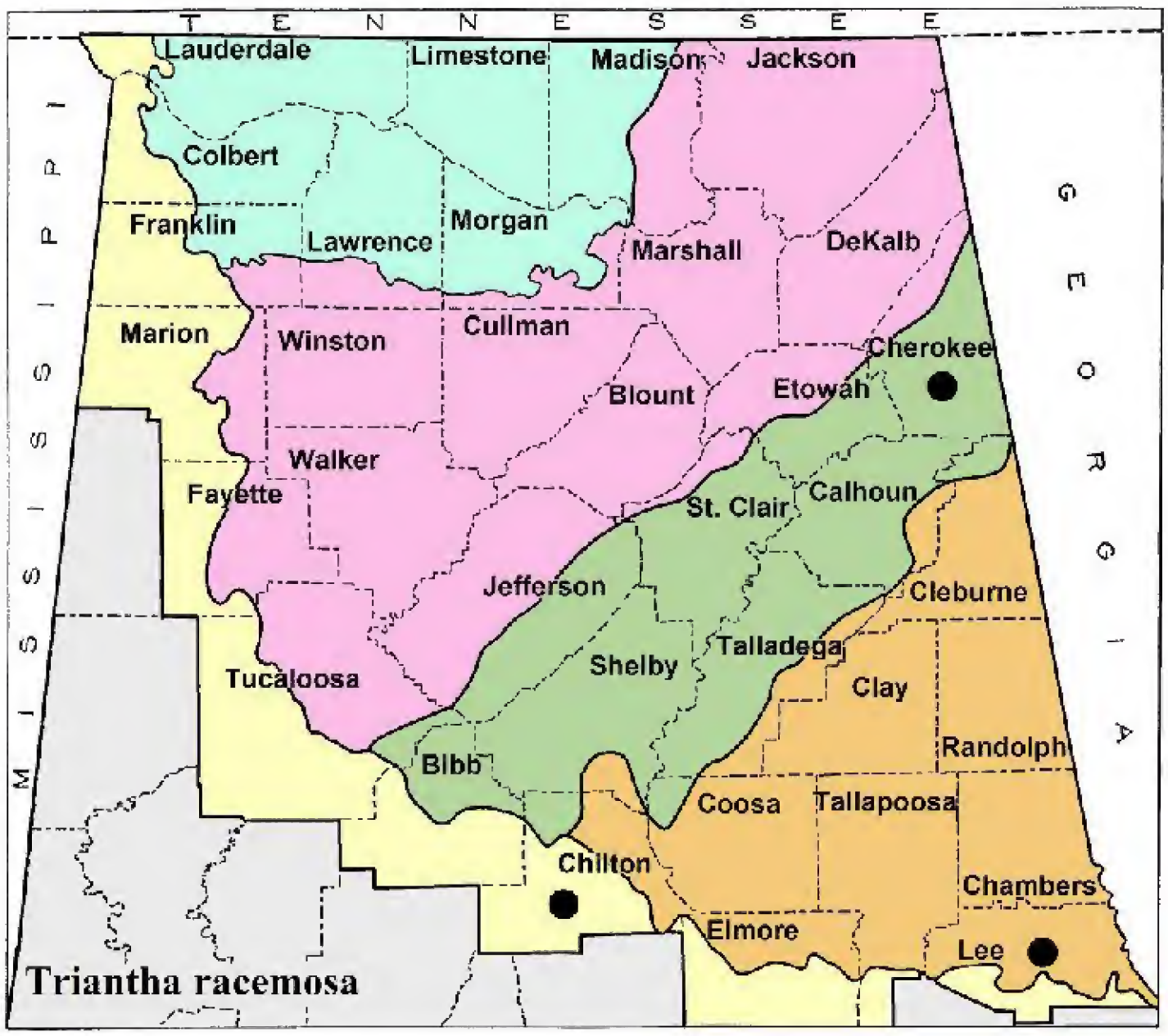


Figure 70. Distribution of *Triantha racemosa* in northern Alabama.

The population of *Triantha racemosa* in Cherokee County occurs in a seepage bog with the Green Pitcher-Plant, *Sarracenia oreophila* (Kearney) Wherry. This site is located in the Coosa Valley district of the Ridge & Valley province portion of the county. There is a historical collection from Lee County (*Baker s.n.*, July 1897) with only "Auburn" on the label, which is in the lower piedmont, but no population has ever been confirmed. This species has been documented from Chilton and Russell counties, which are in the Fall Line Hills district of the upper Coastal Plain. Southern Bog-Asphodel is much more common in southern Alabama in wet sandy-peaty soils of flatwoods, pine savannas, seeps, and bogs. It fruits in late summer to fall (Fig. 71a) and produces capsules, which are slightly longer than or equal to the length of the sepals (Fig. 71b).

(71a) fruiting raceme.

(71b) Close-up of fruit.

Figure 71. *Triantha racemosa,* AMAL, *Spaulding14087a*, Cherokee Co., Alabama, 23 Aug 2018. Photos: Dan Spaulding.

FAMILY 4. ALISMATACEAE (Water-Plantain Family)

1. Inflorescence paniculate, highly branched (compound with many of the primary nodes bearing whorled branches, which are also whorled); pistils in a single ring on a flat receptacle; stamens 6 ..... **1. Alisma**
1. Inflorescence racemose, unbranched (nodes with one whorl of flowers); pistils densely crowded over the entire surface of a globose receptacle, forming a ball-like head; stamens more than 6.

    2. Scapes arching at maturity, becoming prostrate and rooting at nodes, forming plantlets (scapes erect when immature); inflorescences with more than 3 flowers per node; whorls subtended by 3 bracts and several smaller bracteoles; all flowers bisexual; fruiting heads (aggregate of achenes) bur-like due to long, persistent styles; achenes plump (turgid) and longitudinally ribbed, not winged..... **2. Echinodorus**
    2. Scapes erect; fruiting heads not bur-like; inflorescences with 3 flowers per node; whorls subtended by 3 bracts, lacking additional smaller bracteoles; flowers mostly unisexual (lower flowers bisexual in *Sagittaria calycina*); achenes flattened with a lateral wing, not ribbed ..... **3. Sagittaria**

1. ALISMA Linnaeus 1753
[Ancient Greek name of a water plant]

1. Alisma subcordatum Raf. {somewhat heart-shaped} — AMERICAN WATER-PLANTAIN; SOUTHERN WATER-PLANTAIN (Fig. 72). [*Alisma plantago-aquatica* L. ssp. *subcordatum* (Raf.) Hultén; *Alisma plantago-aquatica* var. *parviflorum* (Pursh) Torr.]

Amphibious or emersed aquatic, perennial herb from bulbous corms. Marshes, ditches, wet disturbed areas, shores of ponds, lakes, and streams; flowers and fruits June–October; frequent in the Highland Rim; uncommon in the Cumberland Plateau, Ridge & Valley, and Piedmont; rare in the Coastal Plain (Fig. 73). Endemic to eastern North America, from southern Canada south to Texas and Georgia, excluding Louisiana and Florida (Haynes & Hellquist 2000a).

Figure 72. *Alisma subcordatum*, Benton Co., Tennessee, 5 Jul 2010. Photos: Brian Finzel.

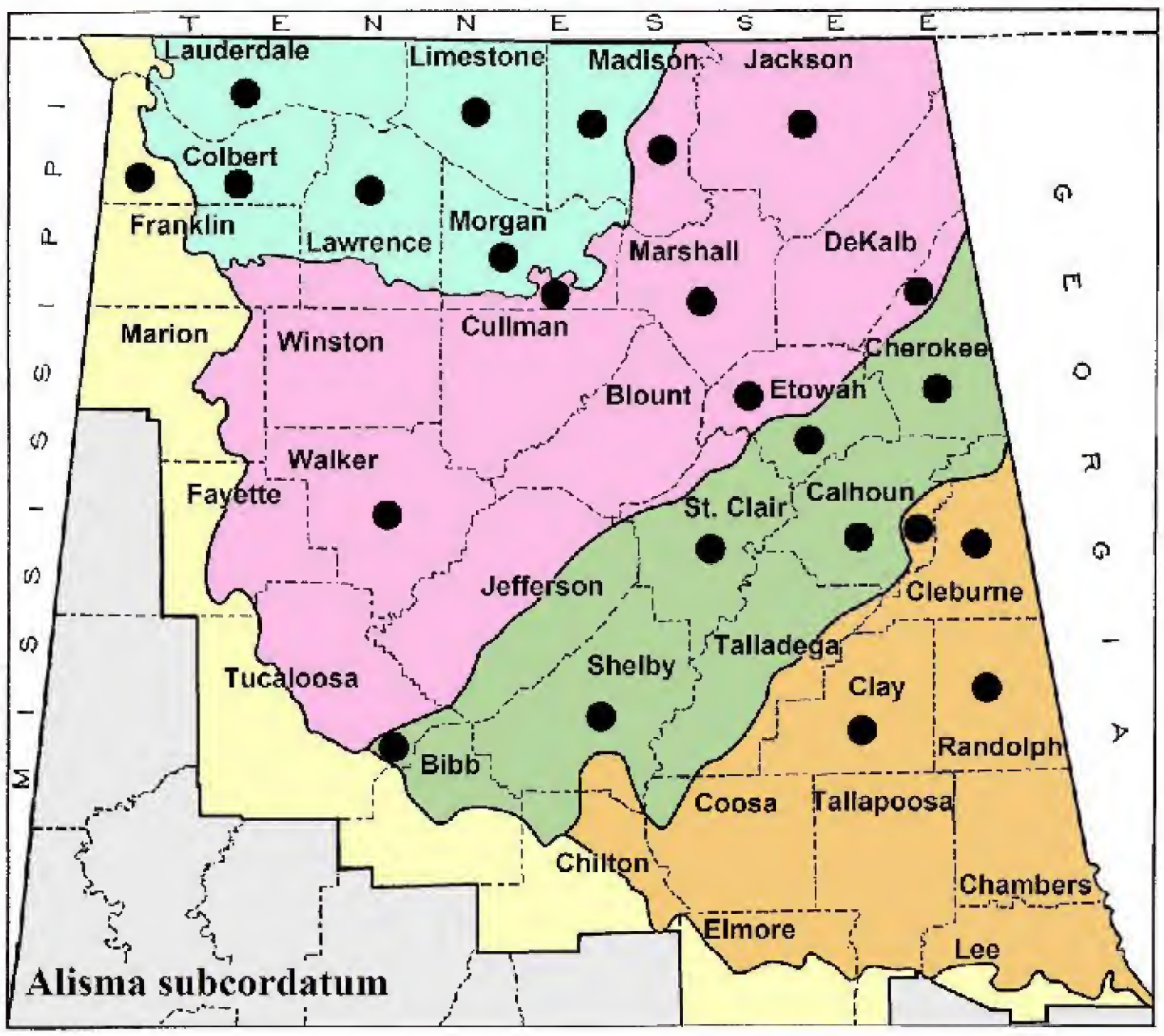


Figure 73. Distribution of *Alisma subcordatum* in northern Alabama.

Alisma is distinguished by its six stamens, highly branched inflorescence, and numerous carpels (pistils) that form a ring on a flat receptacle (Fig. 74a–b). Following pollination, floral receptacles transform into small, thin disks of scaly fruits (Fig. 74c). The spongy tissue of the fruit is well developed and provides buoyancy for aquatic dispersal. When passed through the digestive tract of waterfowl, germination of the achenes is reported to be enhanced (Rogers 1983).

(74a) Ovary side-view. (74b) Ovary top-view. (74c) Ring of achenes.

Figure 74. *Alisma subcordatum.* A–B. Wilson Co., Tennessee, 28 Jul 2014. Photos: Brian Finzel. C. AMAL, *Spaulding 12506*, Cherokee Co., Alabama, 26 Jul 2006. Photo: Dan Spaulding.

At maturity, the bulb-like bases (corms) of water-plantain become filled with starch. Once thoroughly dried, they can be used as a food source (Fernald & Kinsey 1943). Native Americans utilized the corms medicinally to treat various ailments such as heartburn, stomach aches, cramps, constipation, sores, wounds, bruises, and ulcers (Moerman 1998).

2. **ECHINODORUS** L.C. Richard ex Engelmann 1848

[Greek, *echinus*, hedgehog, and *doros*, leather bag; alluding to prickly fruiting head]

1. Echinodorus cordifolius (L.) Griseb. {heart-shaped leaf} — CREEPING BURHEAD; HEART-LEAF SWORD PLANT; RADICANS SWORD (Fig. 75). [*Echinodorus radicans* (Nutt.) Engelm.]

Figure 75. *Echinodorus cordifolius*, pond margin, St. Clair Co., Alabama, 8 Jul 2019. Photos: Dan Spaulding.

Amphibious or emersed aquatic, perennial herb. Swamps, marshes, ditches, margins of ponds, lakes, and streams; flowers and fruits May–October; frequent in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Coastal Plain; uncommon in the Piedmont (Fig. 76). Native throughout the Americas, in the USA known from Maryland, south to peninsular Florida, west to Texas, north through the interior to southern Illinois (Weakley 2015).

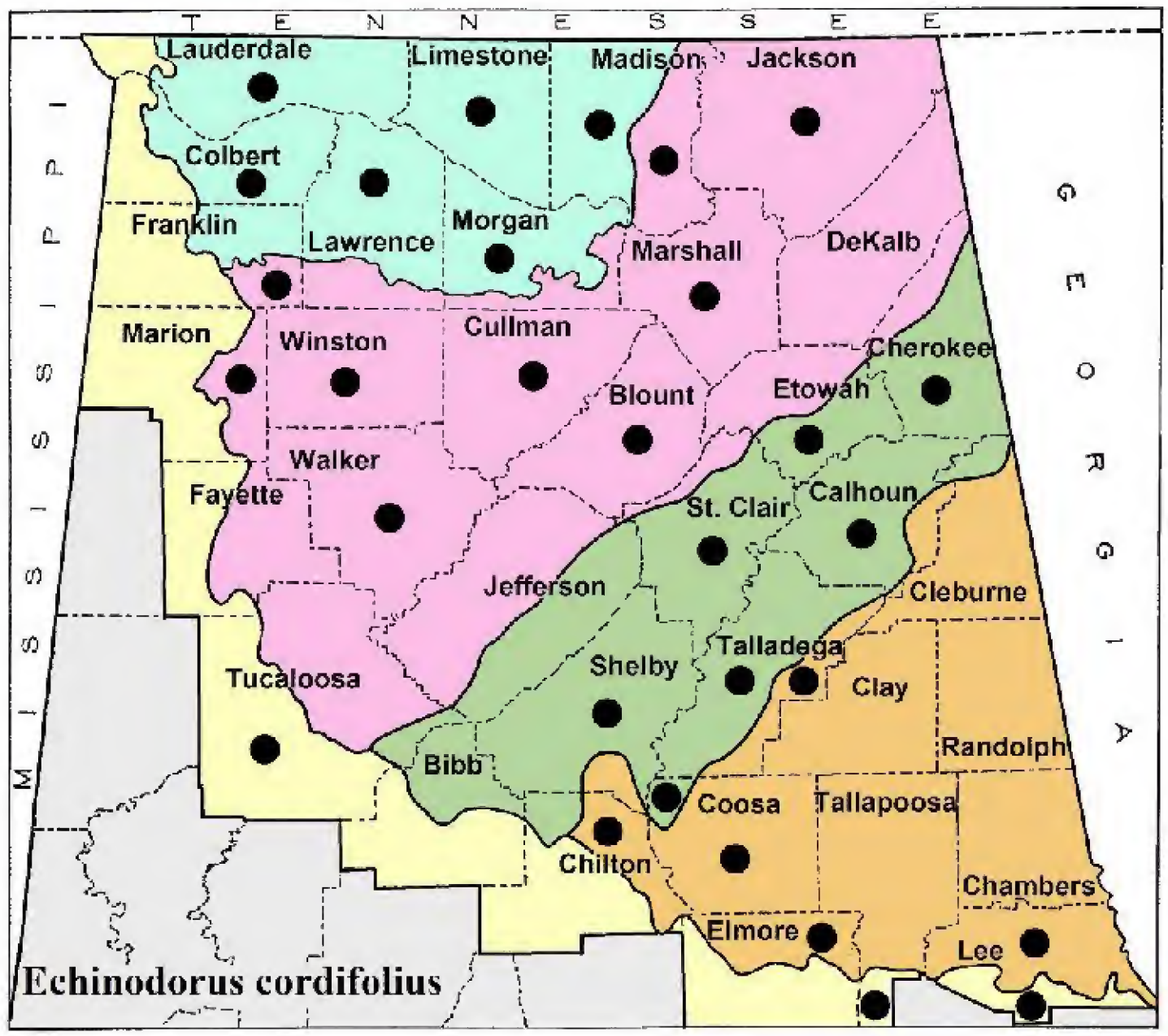


Figure 76. Distribution of *Echinodorus cordifolius* in northern Alabama.

Key characters of *Echinodorus cordifolius* are its arching or decumbent inflorescences that occasionally produce young plantlets at some of the nodes (Fig. 77), sepals with papillose veins, and flowers with over 20 stamens. *Echinodorus berteroi* (Spreng.) Fassett [Upright Burrhead] is similar (Fig. 78a–b) and has been documented from surrounding states, but its main distribution is west of the Mississippi River, ranging south to South America (Haynes & Hellquist 2000a). It differs by its erect, often compound inflorescences, smooth sepals, and flowers with usually only 12 stamens. Beaks of the fruits of *E. berteroi* are longer (Fig. 78c) than the beaks of *E. cordifolius* (Fig. 78d).

Figure 77. *Echinodorus cordifolius* plantlets, Stoddard Co., Missouri, 31 Aug 2017. Photo: Jared Gorrell.

(78a) *Echinodorus berteroi* plant.

(78b) *Echinodorus berteroi* flower close-up.

(78c) *Echinodorus berteroi* fruits.

(78d) *Echinodorus cordifolius* fruits.

Figure 78. A–C. Fulton Co., Kentucky, 8 Jul 2013. Photos: Brian Finzel. D. Inlet to the Tennessee River, Limestone Co., Alabama, 5 July 2017. Photo: Dan Spaulding.

The chopped roots and leaves of *Echinodorus cordifolius* are reported to cause skin blisters if touched (Rogers 1983). This emersed aquatic is available in the aquarium trade for larger aquariums and sold under the name Radicans Sword. It is listed as an invasive species in some countries, where sales may be prohibited (Hoveka et al. 2016).

2. SAGITTARIA Linnaeus 1753

[Latin *sagitta*, arrow; in reference to leaf shape of some species]

1. Emergent leaves with sagittate (arrowhead-like) leaf blades with large basal lobes and distinct petioles; submersed leaves usually absent, except when water level is high.

    2. Sepals appressed in fruit, nearly enclosing the fruiting head; lower whorls of flowers pistillate with a ring of sterile stamens (bisexual), upper flowers staminate, filaments roughened with minute scales; petioles, peduncles, and pedicels thick and spongy..... **2. Sagittaria calycina**
    2. Sepals reflexed or at least widely spreading in fruit and not enclosing the fruiting head; lower whorls of flowers pistillate, lacking stamens (unisexual); upper flowers staminate, filaments glabrous; petioles, peduncles, and pedicels not conspicuously thick and spongy.

        3. Achene beak terminal (extending along the long axis of the achene); inflorescence bracts lanceolate (5–40 mm long) flattened to slightly concave, but not boat-shaped; leaf petioles winged and deeply grooved; leaf blades, petioles, and bracts glabrous or papillate with minute, blunt projections (usually found along leaf margins, main veins, and upper petioles) ..... **1. Sagittaria australis**
        3. Achene beak lateral (at a right angle to the long axis of the achene); inflorescence with boat-shaped bracts (2–14 mm long), which have a concave "hull" and narrow "bow" with obtuse or broadly acute tips; leaf petioles roundish with low ribs, but not distinctly winged or grooved; leaf blades, petioles and bracts glabrous, or densely pubescent (hairs clear and tapering to a point) ..... **4. Sagittaria latifolia**

1. Emergent leaves, if present, with linear, lanceolate, elliptic, or ovate, blades, without well-formed basal lobes (*S. platyphylla* occasionally has small auricles at base of blade), with or without petioles; submersed leaves present and all reduced to phyllodia, which are sessile, bladeless, and linear.

    4. Leaves mostly submersed (rarely emersed); sessile, linear, and bladeless (phyllodial); abaxial wing of fruit scalloped or toothed; plants of the Cumberland Plateau inhabiting riverine shoals and pools in cracks and crevices of sandstone bedrock..... **6. Sagittaria secundifolia**
    4. Leaves submersed and emersed; emergent leaves often with an expanded blade and petiole (submerged leaves phyllodial); abaxial wing of fruit entire; plants widespread and mostly found in marshes, ponds, lakes, and slow-moving streams.

        5. Stalks of fruiting heads, especially on lower whorls, reflexed and often stout at maturity; bracts fused much of their length, free portions broadly triangular and obtuse; emergent leaves often with broadly elliptic to ovate blades, occasionally lanceolate (0.5–7 cm wide); achenes with slender beaks 0.3–0.6 mm long..... **5. Sagittaria platyphylla**
        5. Stalks of fruiting heads ascending or spreading and slender, not noticeably thickened; bracts fused only in the basal half, free portions triangular and acute; emergent leaves bladeless or with narrowly lanceolate to narrowly elliptical leaf blades (up to 2 cm wide); achene beaks less than 0.3 mm long, sometimes absent..... **3. Sagittaria graminea**

1. Sagittaria australis (J.G. Sm.) Small {southern} — LONG-BEAK ARROWHEAD; SOUTHERN ARROWHEAD; APPALACHIAN ARROWHEAD (Fig. 79). [*Sagittaria engelmanniana* J.G. Sm. ssp. *longirostra* auct. non Micheli; *Sagittaria longirostra* (Micheli) J.G. Sm. var. *australis* J.G. Sm.]

Figure 79. *Sagittaria australis*, Jefferson Co., Alabama, 28 Jul 2011. Photo: Brian Finzel.

Amphibious or emersed aquatic, perennial herb with stolons terminated by corms. Marshes, ditches, wet meadows, swamps, sloughs, springs, ponds, mudflats, and streams; flowers and fruits June–October; frequent in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Piedmont; uncommon in the Coastal Plain (Fig. 80). Native to the eastern USA, occurring mostly south of the Ohio River and east of the Mississippi River, but ranging from New Jersey west to Iowa and south to Louisiana and the Panhandle of Florida (Kartesz 2018).

Sagittaria latifolia is often confused with *S. australis* because both species have arrow-head shaped leaves. *Sagittaria australis* can be differentiated by the following characters: achene beaks are terminal, projecting mostly upwards (Fig. 81a); bracts are lanceolate (Fig. 81b); petioles are deeply grooved or winged (Fig. 81c); and plants lack pubescence, but often have white papillae on the margins of the leaves and petioles (Fig. 81d).

Sagittaria engelmanniana [Engelmann's Arrowhead] is also mistaken for *S. australis* because its leaves, bracts, and achene beaks are somewhat similar. Engelmann's Arrowhead differs by the following characteristics: rounded petioles; leaves that are often narrowly sagittate; lowest leaves frequently lacking basal lobes (both leaf types are often present on an individual plant); flowers in 2–4 whorls; achenes with facial wings extending onto the beaks (Beal et al. 1982). *Sagittaria engelmanniana* is chiefly a Coastal Plain species, reports of it occurring in northern Alabama are likely erroneous.

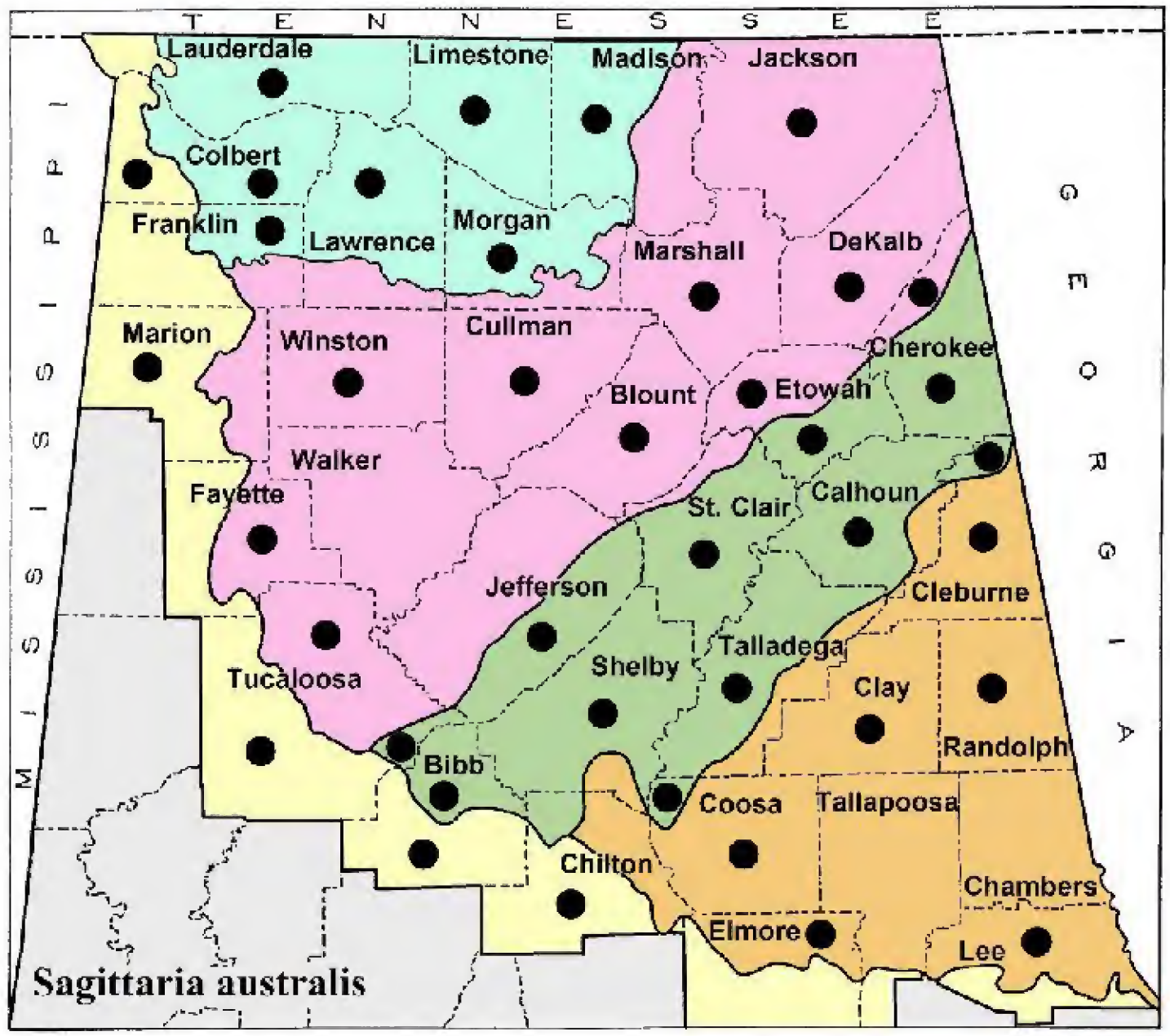


Figure 80. Distribution of *Sagittaria australis* in northern Alabama.

(81a) Achene beaks terminal.

(81b) Bracts lanceolate.

(81c) Winged/grooved petiole.

(81d) White papillate petiole.

Figure 81. *Sagittaria australis*. A–B. Madison Co., Alabama, 7 Sep 2015. Photos: Brian Finzel. C–D. Etowah Co., Alabama, 11 Aug 2018. Photos: Dan Spaulding.

2. Sagittaria calycina Engelm. {with conspicuous calyx} — HOODED ARROWHEAD; LONG-LOBE ARROWHEAD; THICK-STALK ARROWHEAD (Fig. 82). [*Lophotocarpus calycinus* (Engelm.) J.G. Sm.; *Sagittaria montevidensis* Cham. & Schlecht. ssp. *calycina* (Engelm.) Bogin]

Figure 82. *Sagittaria calycina* [with *Heteranthera limosa* (Sw.) Willd.], Tennessee National Wildlife Refuge, Humphreys Co., Tennessee, 8 Aug 2010. Photo: Brian Finzel.

Amphibious or emersed aquatic, perennial herb. Mudflats, marshes, ditches, wet meadows, swamps, sloughs, springs, borders of ponds, rivers, lakes, and streams; flowers and fruits June–October; uncommon in the Highland Rim and upper Coastal Plain; rare in the Cumberland Plateau; very rare in the Ridge & Valley (Fig. 83). Native chiefly to the central USA, ranging from Colorado to south Dakota, east to southwest Virginia, south to northern Georgia, west to Louisiana and Texas; disjunct in California and Mexico (Haynes & Hellquist 2000a). Introduced into Australia, where it is considered to be an invasive, noxious weed (Adair et al. 2012).

Sagittaria calycina is vegetatively similar to *S. australis* and *S. latifolia* because of its arrowhead shaped leaves, but the leaf stalks (petioles) of *S. calycina* are very thick and spongy (Fig. 84a). When fertile, *S. calycina* can be identified by its bisexual lower whorls of flowers, which have a ring of sterile stamens around fertile pistils (Fig. 84b). Its peduncles and pedicels are also thick and spongy. In fruit, its sepals are appressed and completely surrounding the fruiting head (Fig. 84c).

Sagittaria calycina has been recognized as a subspecies of *S. montevidensis* by some authors (Bogin 1955; Haynes & Hellquist 2000a). Keener (2005) elevated *S. montevidensis* subsp. *calycina* to species rank with two varieties, var. *calycina* and var. *spongiosa* Engelm. Weakley (2015) treats *S. calycina* var. *spongiosa* as a distinct species, *S. spathulata* (J.G. Sm.) Buch. [Tidal Arrowhead]. This taxon has only phyllodial leaves, lacking expanded blades. Tidal Arrowhead occurs in tidal mudflats along the coast from New Brunswick to North Carolina. *Sagittaria montevidensis* [Giant Arrowhead] is similar to *S. calycina* but differs by having purple-red spots at the base of the petals and lacking a ring of non-functioning stamens in the pistillate flowers. Giant Arrowhead is native to South America and is occasionally found near old seaports in the southeastern USA.

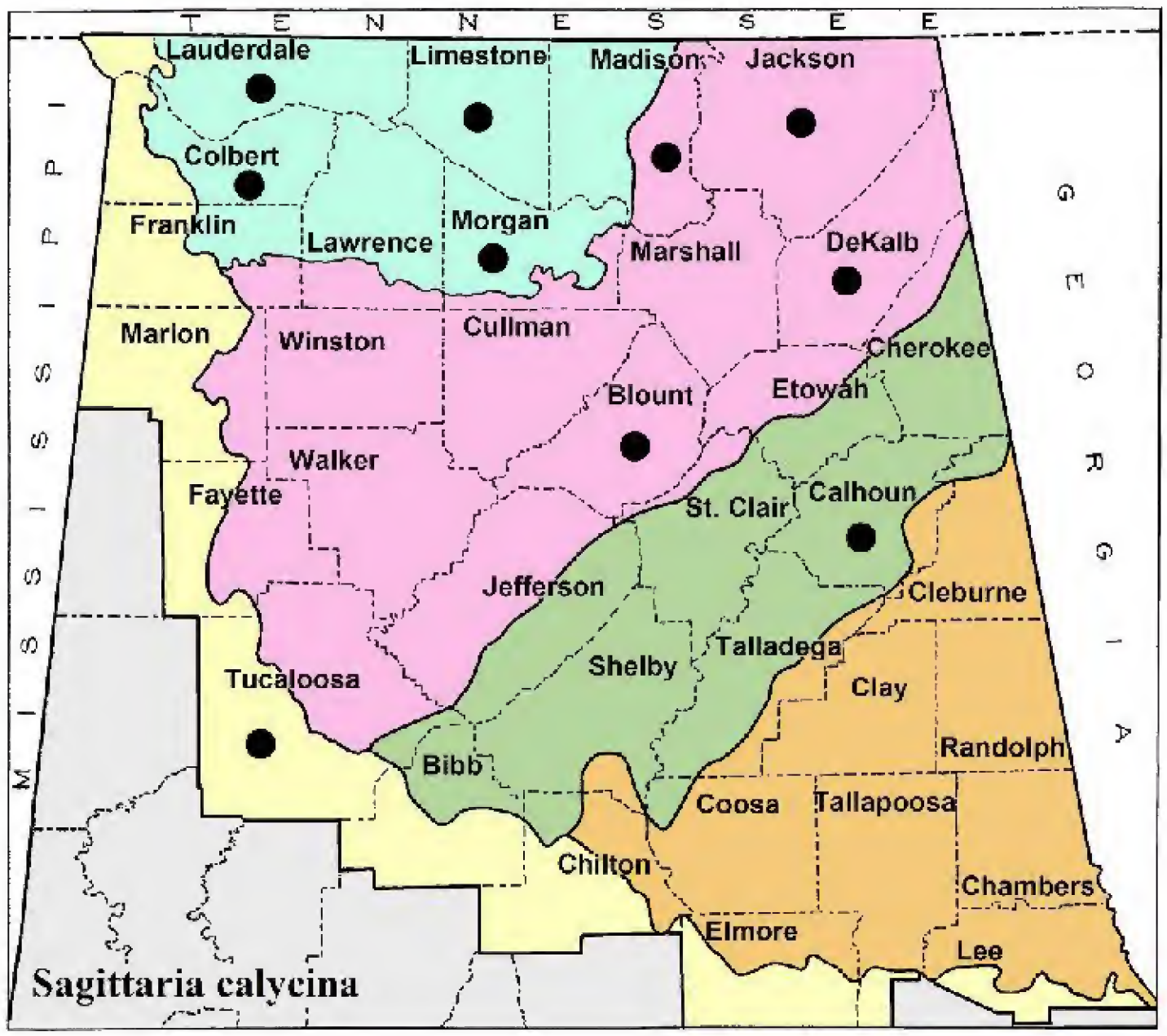


Figure 83. Distribution of *Sagittaria calycina* in northern Alabama.

(84a) Thick, spongy petioles & peduncles. (84b) Bisexual flowers in lower whorl. (84c) Calyx enclosing fruits.

Figure 84. *Sagittaria calycina.* A–C. Mud flat along Paint Rock River, Madison Co., Alabama, 6 Oct 2018. Photos: Dan Spaulding.

3. Sagittaria graminea Michx. {grass-like} — GRASSLEAF ARROWHEAD; GRASSY ARROWHEAD; LANCE-LEAF ARROWHEAD (Fig. 85). [*Sagittaria cycloptera* (J.G. Sm.) C. Mohr; *Sagittaria eatonii* J.G. Sm.]

Figure 85. *Sagittaria graminea*, Gulf Co., Florida, 28 Mar 2015. Photos: Brian Finzel.

Emersed aquatic, perennial herb with rhizomes. Pond and lake margins, also marshes, ditches, seeps, wet flatwoods, swamps, and bogs in southern Alabama; flowers and fruits late March–November; very rare in the Piedmont; frequent in the lower Coastal Plain (Fig. 86). Native to eastern North America, ranging from the West Indies to Nova Scotia west to Ontario and south to east Texas, but mostly near the coast in the South (Kartesz 2018).

The only valid specimen known of *Sagittaria graminea* within the study area was collected from Lee County, near Auburn, along the shores of Lake Condy on May 25, 1962. *Sagittaria graminea* has been reported from northern Alabama (Wooten 1973), but all such specimens examined have been annotated to *S. platyphylla,* which is a member of the *S. graminea* complex.

Sagittaria graminea has slender, ascending fruiting stalks (Fig. 87a) and the free portion of its bracts are acute. A similar species, *S. platyphylla*, has stout, reflexed fruiting stalks and the free portions of its bracts are obtuse. *Sagittaria platyphylla* typically has broader leaf blades than *S. graminea*, but they can also be lanceolate, so this character is unreliable. Both species have basally dilated filaments and smooth sepals and bracts (Fig. 87b). *Sagittaria lancifolia* L. subsp. *media* (Micheli) Bogin, which is found on the Coastal Plain, can be confused with these members of *S. graminea* complex, but its filaments are cylindric and its bracts and sepals are papillose (Fig. 87c).

Sagittaria chapmanii (J.G. Sm.) C. Mohr is another species within the *S. graminea* complex and occurs in southeast Alabama (Brian Keener, pers. comm. 2019). It usually has branched inflorescences, whereas those of *S. graminea* are usually unbranched. However, since both species can have either panicles or racemes (Brian Keener, pers. comm. 2019), it is best to examine their bracts. Those of *S. graminea* (Fig. 88a) are basally connate (fused) with acute free tips while those of *S. chapmanii* (Fig. 88b) are only slightly connate with acuminate free tips (Weakley 2015).

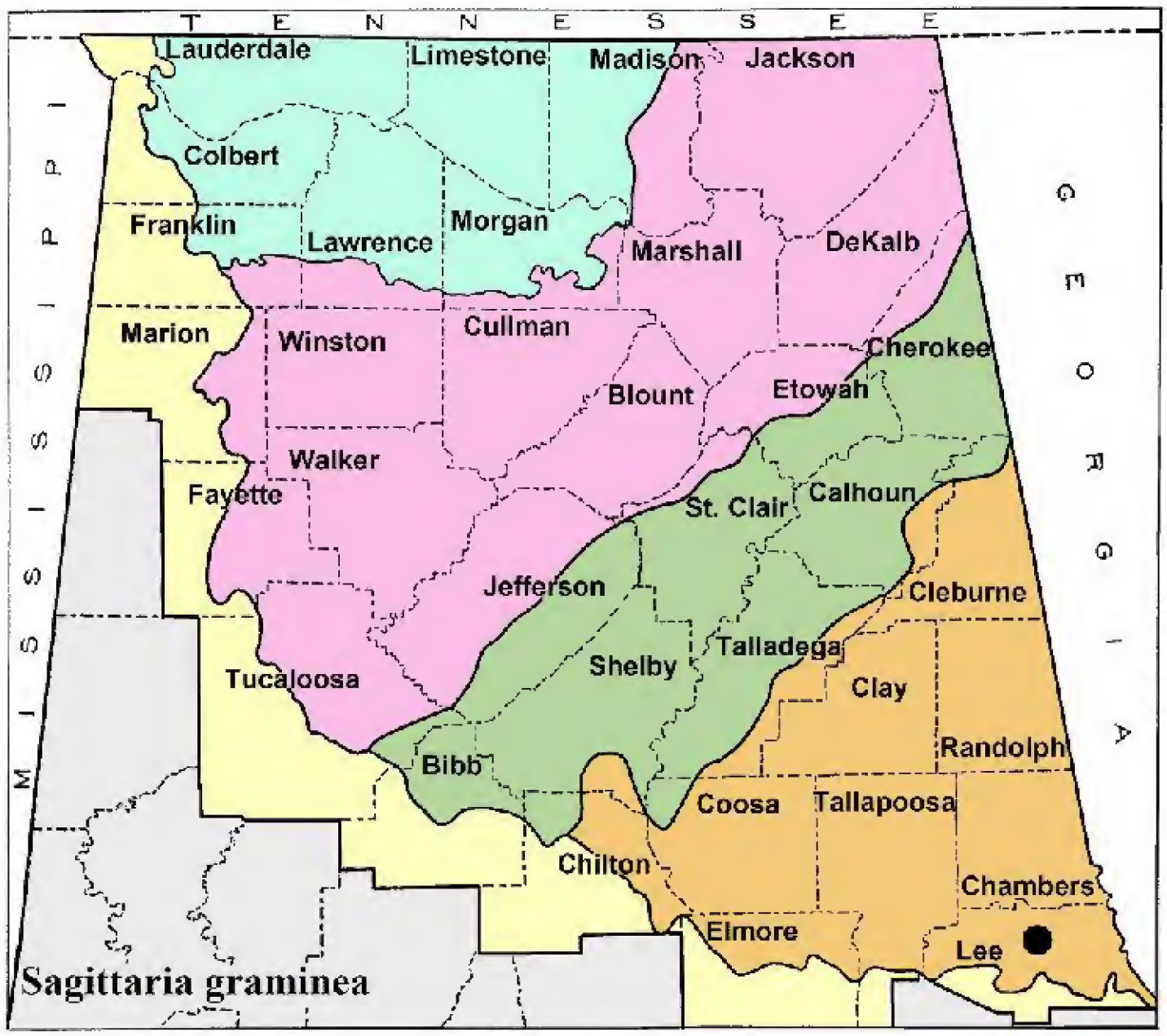


Figure 86. Distribution of *Sagittaria graminea* in northern Alabama.

(87a) *Sagittaria graminea* pedicels. (87b) *S. graminea* sepals. (87c) *S. lancifolia* subsp. *media* sepals.

Figure 87. A. Pinellas Co. Florida, 28 Mar 2019. Photo: Alexander de la Paz. B–C. Gulf Co., Florida, 28 Mar 2015. Photos: Brian Finzel

(88a) *Sagittaria graminea* bracts. (88b) *Sagittaria chapmanii* bracts.

Figure 88. A. AMAL, *Diamond 17465*, Butler Co., Alabama, 29 Apr 2007. B. AMAL, *Kral 91856*, Houston Co., Alabama, 17 Sep 2001. Photos: Dan Spaulding.

4. Sagittaria latifolia Willd. {broad-leaved} — BROADLEAF ARROWHEAD; DUCK-POTATO; WAPATO (Fig. 89). [*Sagittaria latifolia* var. *pubescens* (Muhl. ex Nutt.) J.G. Sm.; *Sagittaria obtusa* Muhl. ex Willd., non Thunb.; *Sagittaria planipes* Fern.; *Sagittaria pubescens* Muhl. ex Nutt.; *Sagittaria viscosa* C. Mohr]

Figure 89. *Sagittaria latifolia*, Leon County, Florida, 25 Nov 2018. Photos: Anthony Melton.

Amphibious or emersed aquatic, perennial herb with stolons terminated by corms. Marshes, swamps, ditches, wet pastures, mudflats, margins of ponds, lakes, rivers, and streams; flowers and fruits late May–November; uncommon in the Highland Rim, Cumberland Plateau, and Ridge & Valley; frequent in the Piedmont and Coastal Plain (Fig. 90). This is the most widespread species of the genus in the New World, ranging from Canada south through the entire USA to northern South America (Rogers 1983).

Key characteristics of *Sagittaria latifolia* are its lateral achene beaks that are frequently hooked (Fig. 91a) and its boat-shaped bracts (Fig. 91b). When sterile, *S. latifolia* can be distinguished from *S. australis* by its petioles, which have slightly have raised ribs (Fig. 92), whereas *S. australis* has petioles that are distinctly winged or grooved. Broadleaf Arrowhead can be glabrous or pubescent, but most individuals observed in northern Alabama are pubescent (Fig. 91b–c). Bogin (1955) and Weakley (2015) have recognized *S. latifolia* var. *pubescens*, which is conspicuously pubescent, especially on the leaves and bracts. Haynes & Hellquist (2000a) believe this character is insufficient to justify varietal recognition. Weakley (2015), however, notes that the two varieties also "can be separated by the presence (var. *latifolia*) or absence (var. *pubescens*) of resin-ducts on the achene-faces."

Wapato is a native North American Indian name, referring to their corms (Fernald & Kinsey 1943). Indians were reported to harvest the tubers by wading in the mud and pulling them off with their toes (Gibbons 1962). Corms are produced at the end of the growing season and prepared like

potatoes. These starchy storage organs are considered to be delicious but are only edible after being boiled or baked (Peterson 1977). If eaten raw they are acrid and reported to be toxic (Rogers 1983). The achenes ("seeds") and tubers are eaten by wildlife, especially waterfowl and muskrats (Martin et al. 1951). *Sagittaria latifolia* is cultivated as an emergent aquatic for ornamental ponds.

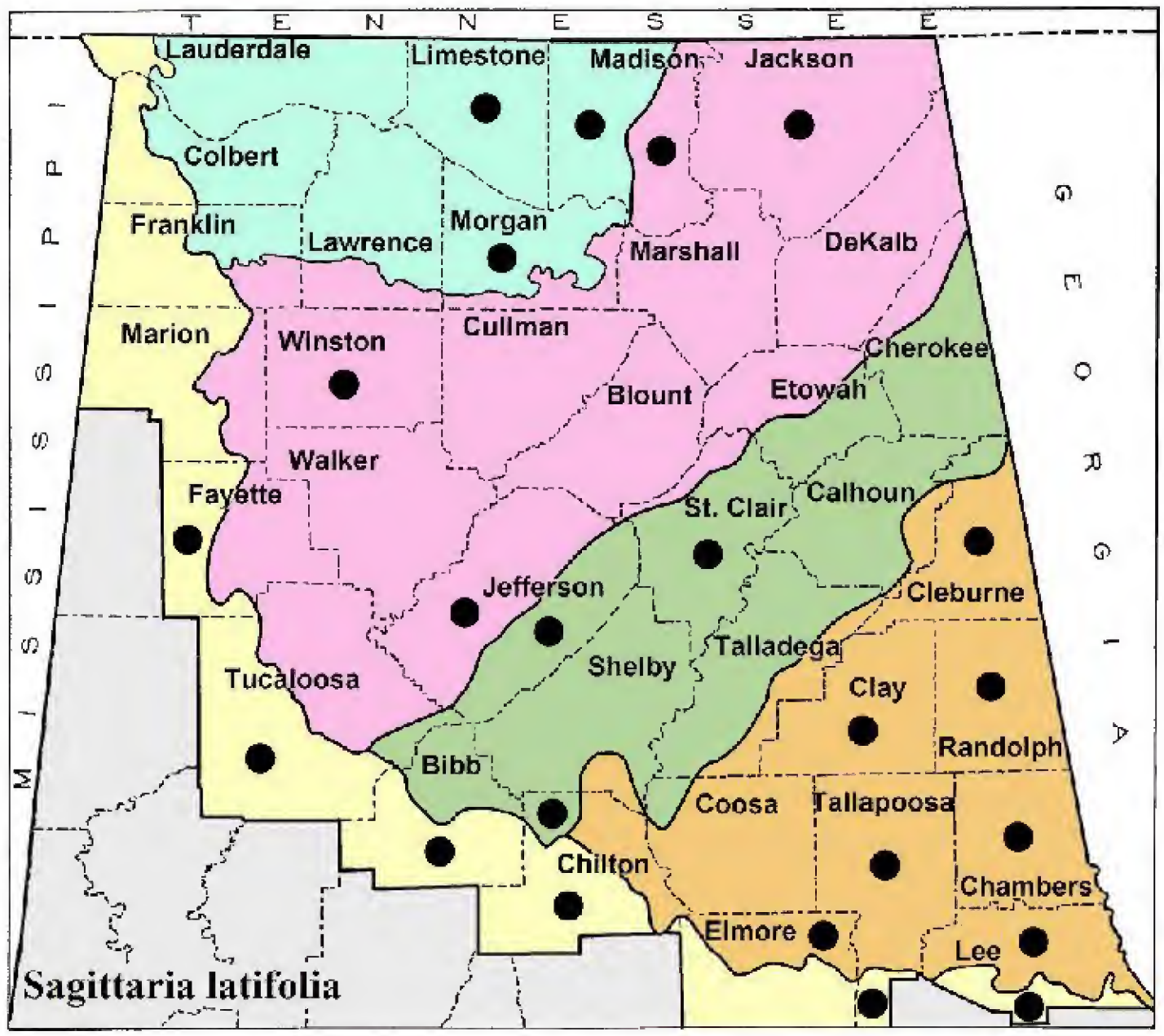


Figure 90. Distribution of *Sagittaria latifolia* in northern Alabama.

(91a) Beaks lateral. (91b) Bracts boat-shaped. (91c) Pubescent rachis. (91d) Hairy leaf and petiole.

Figure 91. *Sagittaria latifolia.* A. Fruiting head with achenes, Morgan Co., Alabama, 5 Oct 2016. Photo: Brian Finzel. B. Fayette Co., Tennessee, 25 Jun 2012. Photo: Brian Finzel. C. Chambers, Co., Alabama, 28 Jul 2018. Photo: Dan Spaulding. D. Jefferson Co., Alabama, 16 Aug 2018. Photo: Dan Spaulding.

Figure. 92. *Sagittaria latifolia* petiole, Cleburne Co., Alabama, 4 Jun 2019. Photo: Dan Spaulding.

5. Sagittaria platyphylla (Engelm.) J.G. Sm. {wide-leaved} — DELTA ARROWHEAD; DELTA DUCK-POTATO (Fig. 93a–b). [*Sagittaria graminea* Michx. var. *platyphylla* Engelm.; *Sagittaria mohrii* J.G. Sm.]

(Fig. 93a) Photo: Brian Finzel.

(Fig. 93b) Photo: Dan Spaulding.

Figure 93. *Sagittaria platyphylla* [with *Justicia americana* (L.) Vahl.]. A. North River Rock Quarry Park, Tuscaloosa Co., Alabama, 26 May 2012. B. Lake Purdy, Jefferson Co., Alabama, 16 Jul 2018.

Emersed aquatic, perennial herb with stolons and corms. Marshes, swamps, sloughs, springs, margins of ponds, lakes, and rivers; flowers and fruits late May–October; frequent in the Interior Low Plateau, Cumberland Plateau, and western Coastal Plain; uncommon in the Ridge & Valley and Piedmont (Fig. 94). Native to eastern North America, its primary range extending from central Texas to the Panhandle of Florida north to Oklahoma, southern Illinois, and Kentucky, with scattered populations in other eastern states (Haynes & Hellquist 2000a). The species has been introduced into South Africa and Australia, where it is considered to be an invasive weed (Kwong et al. 2017).

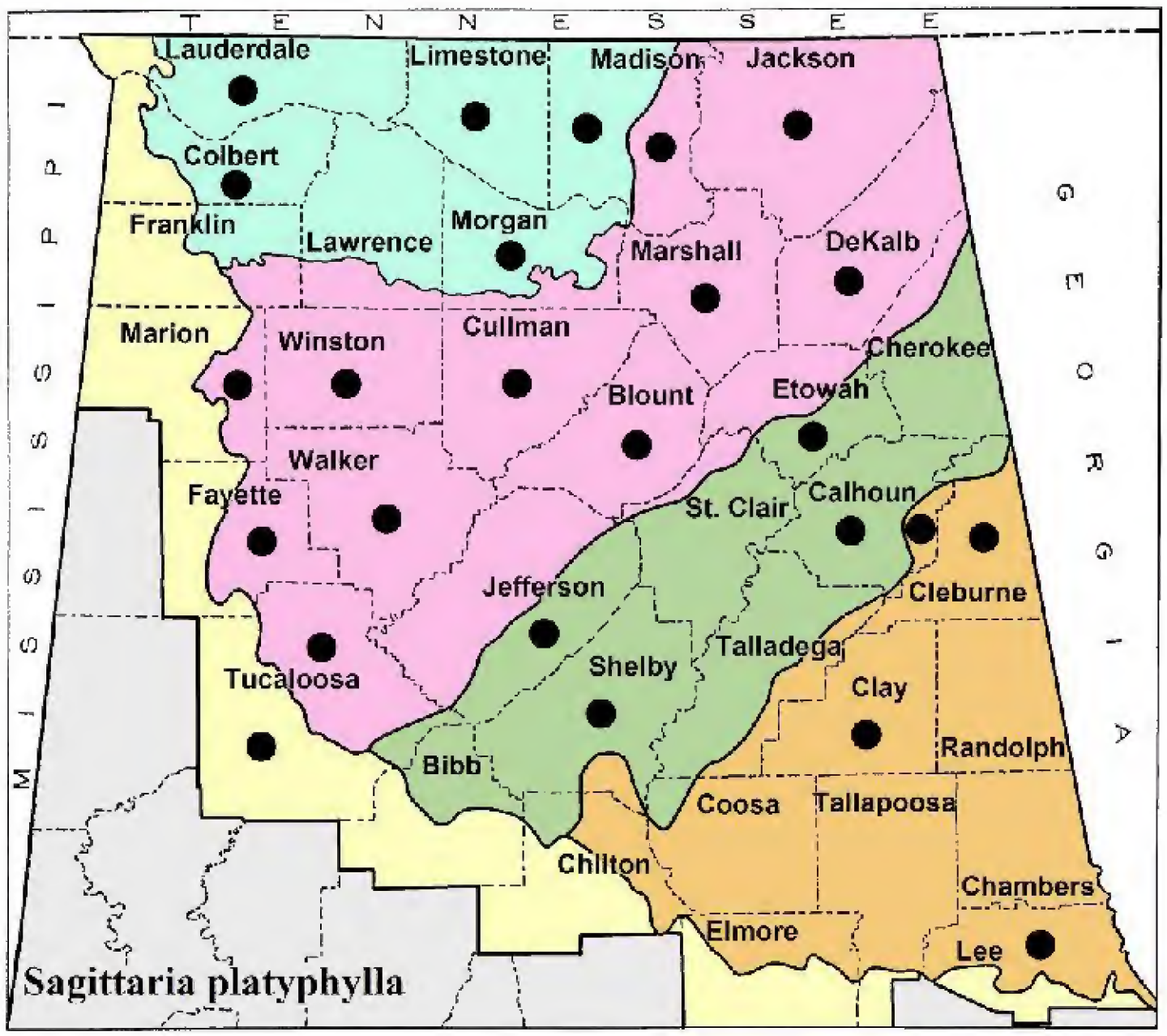


Figure 94. Distribution of *Sagittaria platyphylla* in northern Alabama.

Sagittaria platyphylla is a member of the *S. graminea* complex (Hauber & Legé 1999). It can be distinguished from closely related species by its distinctly connate (fused) bracts with obtuse free tips (Fig. 95) and by its mature fruiting stalks, which are thickened and usually reflexed (Fig. 96a). The leaf blades of *S. platyphylla* are typically broadly elliptic, or ovate, but can be lanceolate, resembling leaves of *S. graminea*. A population of *S. platyphylla* will occasionally have some individuals with narrow leaves (Fig. 96b), which can result in misidentification. This species often occurs in dense colonies along shores of ponds, lakes, and rivers (Fig. 96c).

Figure 95. *Sagittaria platyphylla* flowers and bracts, Marshall Co., Alabama, 9 Oct 2014. Photos: Brian Finzel.

(96a) Pedicels thick and often reflexed. (96b) Lanceolate leaved plant. (96c) Dense population along shore.

Figure 96. *Sagittaria platyphylla*. A. Fulton Co., Kentucky, 5 Aug 2013. Photo: Brian Finzel. B. Pond in DeKalb County, Alabama, 11 Aug 2018. Photo: Dan Spaulding. C. Pond in Helena, Shelby County, Alabama, 19 Jul 2018. Photo: Dan Spaulding.

6. Sagittaria secundifolia Kral {leaves on one side} — KRAL'S WATER-PLANTAIN; LITTLE RIVER ARROWHEAD; LITTLE RIVER WATER-PLANTAIN (Fig. 97a–b).

(97a) Photo: Alan Cressler. (97b) Photo: Wayne Barger.

Figure 97. *Sagittaria secundifolia*. A. East Fork of Little River, Chattooga Co., Georgia, 9 Jun 2011. B. West Fork of Little River, DeKalb Co., Alabama 17 Jul 2008.

Submersed aquatic, perennial herb with rhizomes. Cracks in bedrock of streams; flowers and fruits May–August; rare in the Cumberland Plateau; very rare in the Piedmont (Fig. 98). Endemic to northern Alabama, southeast Tennessee, and northwest Georgia (Weakley 2015).

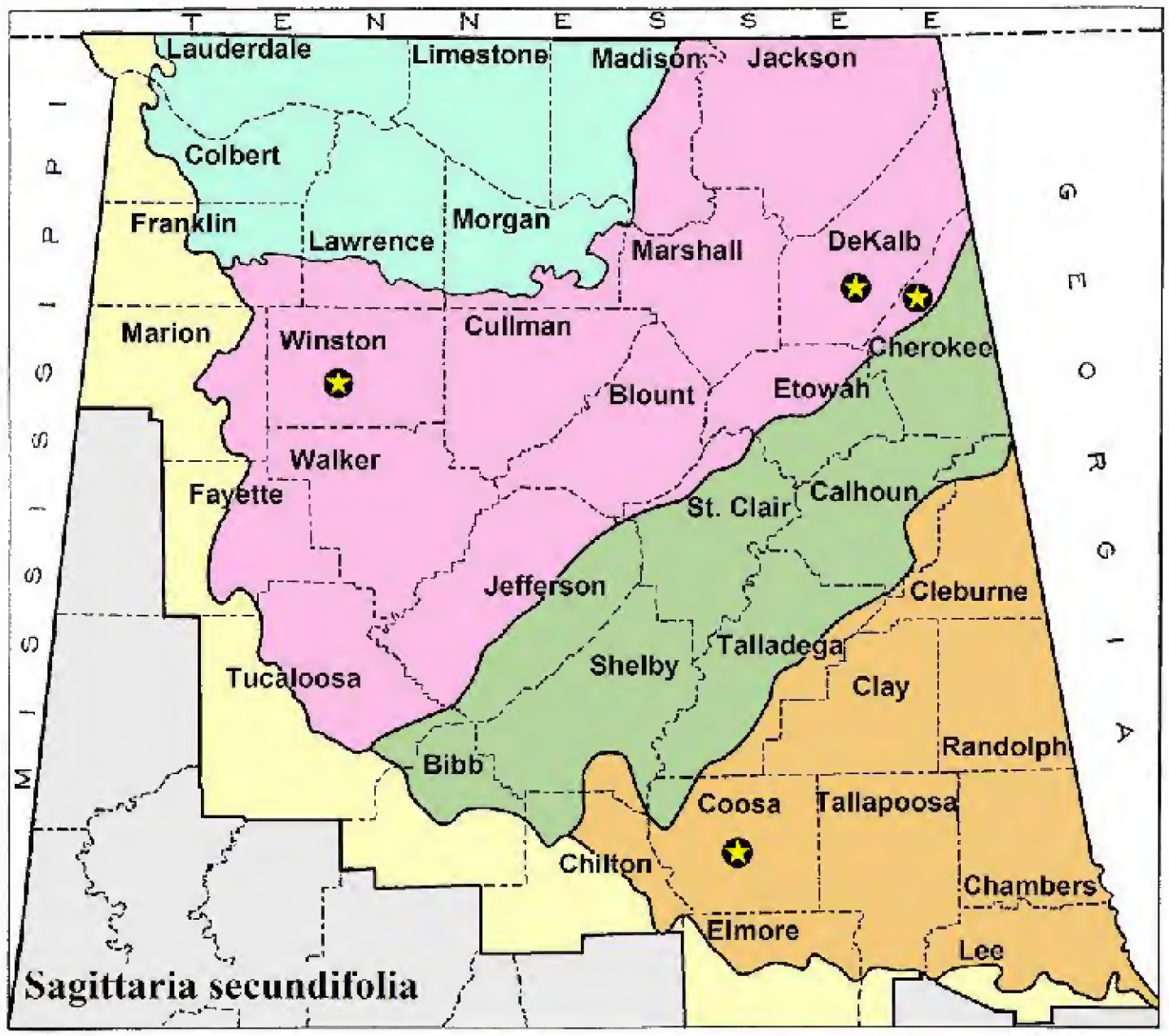


Figure 98. Distribution of *Sagittaria secundifolia* in northern Alabama.

Sagittaria secundifolia has submersed, strap-like, bladeless leaves (phyllodia), and plants are anchored by its rhizomes in rock crevices and streambeds (Fig. 99). In late spring or summer, when the water level is low, flower stalks (peduncles) project above the water surface where pollination occurs (Haynes & Hellquist 2000a). This species was first described by Robert Kral (1982) from collections made in the Little River drainage of Cherokee and DeKalb counties. Kral first observed specimens in the Vanderbilt herbarium collected by A.W. Cusick in 1972, which were misidentified as *S. graminea*. Kral noted that "they were different enough in appearance to be taxonomically provocative." He revisited the site in July 1977 to establish a better understanding of the species. Roland Harper unknowingly collected *S. secundifolia* in DeKalb County on June 6, 1951. Kral's Water-Plantain was federally listed by the U.S. Fish and Wildlife Service as a threatened species in 1990. <https://ecos.fws.gov/ecp0/profile/speciesProfile?sId=8235>

Once published, this new species was on the "radar" of many Alabama botanists. In July 1986, David Whetstone, a professor at Jacksonville State University, discovered a new population in adjacent Chattooga Co., Georgia (Whetstone et al. 1987). In 1992–1993, Scott Gunn, of the Alabama Natural Heritage Program, reported it from along the Sipsey River in Winston County in the Bankhead National Forest (Al Schotz, pers. comm. 2017). In May 2001, Steve Threlkeld and Eric Soehren (2003) discovered the only known population in the Piedmont from Coosa County. They were canoeing and surveying through shoals on Hatchet Creek and noticed *Sagittaria secundifolia*

growing in bedrock crevices of shallow water (Eric Soehren, pers. comm. 2019). Weakley (2015) reports the species occurring in the mountains of southeastern Tennessee.

Figure 99. *Sagittaria secundifolia* in bedrock cracks, DeKalb Co., Alabama 17 Jul 2008. Photo: Wayne Barger.

FAMILY 5. HYDROCHARITACEAE (Frog's-Bit Family)

Prior to the use of molecular techniques, *Najas* was placed exclusively into Najadaceae, a monotypic family. It was thought to be taxonomically distinct because of its reproductive structures. It had hypogynous (superior) ovaries, a single carpel possessing a single ovule, and basal placentation. Hydrocharitaceae sensu stricto differed by having epigynous (inferior) ovaries, 2 to 15 carpels with many ovules, and parietal placentation (Tanaka et al. 1997). However, Shaffer-Fehre (1991) suggested that Najadaceae be merged into Hydrocharitaceae based on similarities in seed coat structure. Modern phylogenetic analyses have consistently shown that *Najas* is clearly nested within the Hydrocharitaceae (Les et al. 1997; Tanaka et al. 1997; Ito et al. 2017) and this is now accepted by many contemporary authors (Stevens 2001; Chase 2004; Reveal 2012; Weakley 2015; APG 2016; Soltis et al. 2018).

1. Leaves in basal rosettes, either ribbon-like (>10 cm long) or petiolate with an expanded blade; stems short (< 2 cm long).

    2. Leaves sessile; blades linear and elongate (> 7 cm long); plants submersed and rooted in substrate; fruiting peduncles coiled and long (> 5 cm long) ..... **6. Vallisneria**
    2. Leaves with distinct petioles; blades suborbicular to ovate (< 7 cm long); plants emersed, rooting in substrate or free floating; fruiting peduncles recurved and shorter (< 6 cm long), not coiled ..... **4. Limnobium**

1. Leaves cauline, mostly linear, but not ribbon-like (< 4 cm long); stems elongate (> 3 cm long).

3. Leaves mostly opposite (sometimes appearing whorled); leaf base expanded and sheath-like; flowers sessile or almost so, and borne underwater; perianth absent (lacking sepals and petals), staminate flowers with 1 stamen ..... **5. Najas**
3. Leaves distinctly in whorls of 3 or more; leaf base not expanded or sheath-like; flowers on thread-like stalks 3–6 cm long; perianth present, staminate flowers with 3–9 stamens.

    4. Leaf margins with conspicuous spiny teeth; midvein of lower leaf surface often with conical bumps tipped with prickles; petals greenish; stamens 3; tubers often present ..... **3. Hydrilla**
    4. Leaf margins with inconspicuous fine teeth; midvein of lower leaf surface lacking bumps or prickles; petals translucent; stamens 7–9; tubers absent.

        5. Midstem leaves 1.5–3 cm long and usually in whorls of 4–6; petals showy, 8–11 mm long and longer than sepals ..... **1. Egeria**
        5. Midstem leaves 0.5–1.3 cm long and in whorls of 3; petals somewhat inconspicuous, 2.5–5 mm long and about as long as sepals ..... **2. Elodea**

1. EGERIA Planchon 1849

[Latin *egeri*, a mythical water nymph, alluding to its aquatic habitat]

1. Egeria densa Planch. {dense} — BRAZILIAN WATERWEED; COMMON WATERWEED; BRAZILIAN ELODEA (Fig. 100). [*Anacharis densa* (Planch.) Victorin; *Elodea densa* (Planch.) Caspary; *Philotria densa* (Planch.) Small & St. John]

Figure 100. *Egeria densa* (in Three Mile Creek), Mobile Co., Alabama, 15 Apr 2008. Photo: Howard Horne.

Submersed aquatic, perennial herb. Lakes, ponds, springs, swamps, sluggish waters of streams and rivers; flowers April–November; uncommon in the Highland Rim and Coastal Plain; rare in the Cumberland Plateau, Ridge & Valley, and Piedmont (Fig. 101). Native to Brazil and introduced around the world in countries with mild climates, although individual plants have been reported to survive temporarily under ice (Haynes 2000a). This species is widely sold in the aquarium trade (as *Elodea* or *Anacharis*) and has escaped throughout much of North America, Europe, Africa, Asia, Australia, and New Zealand (Haynes & Holm-Nielsen 2001).

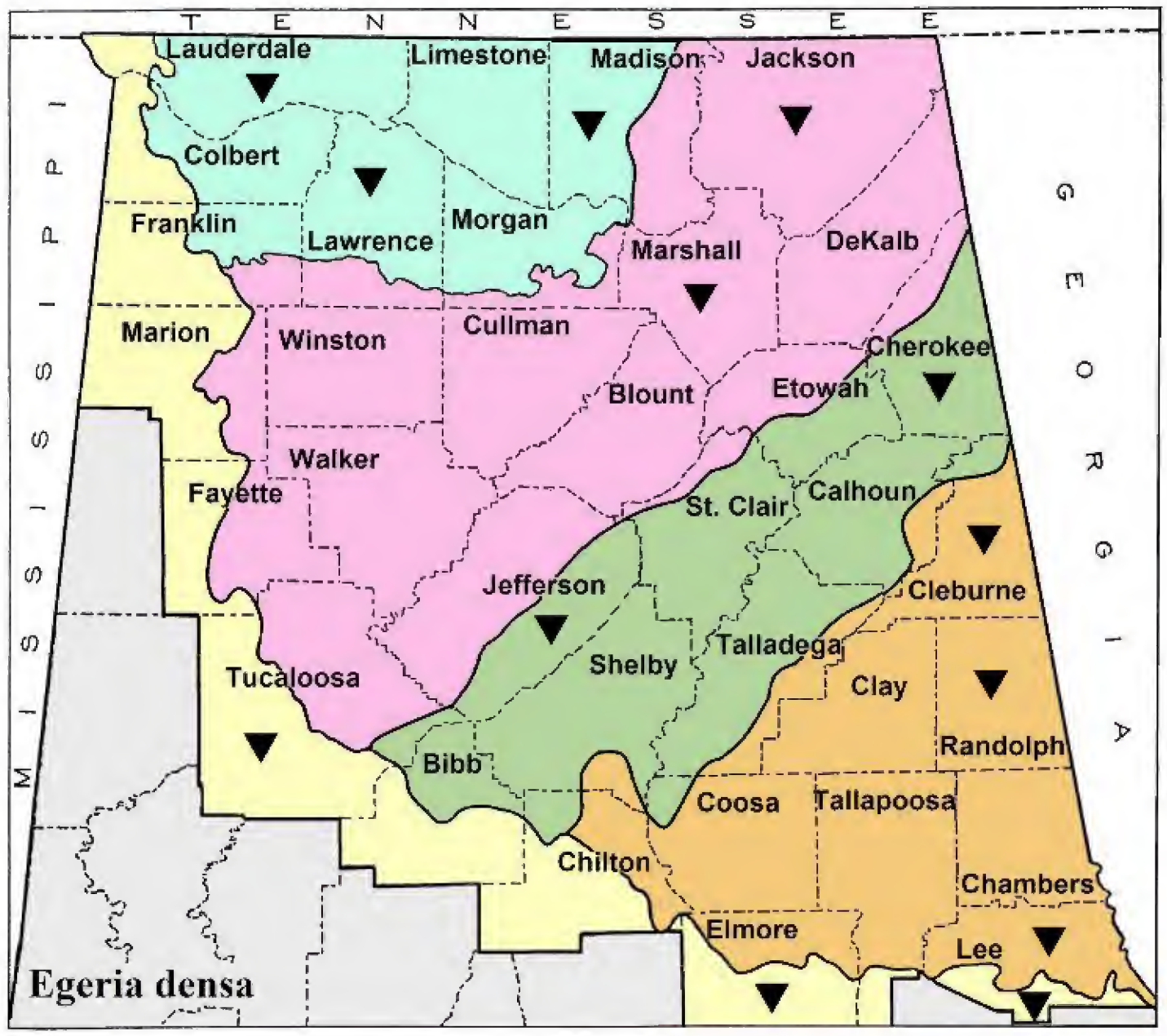
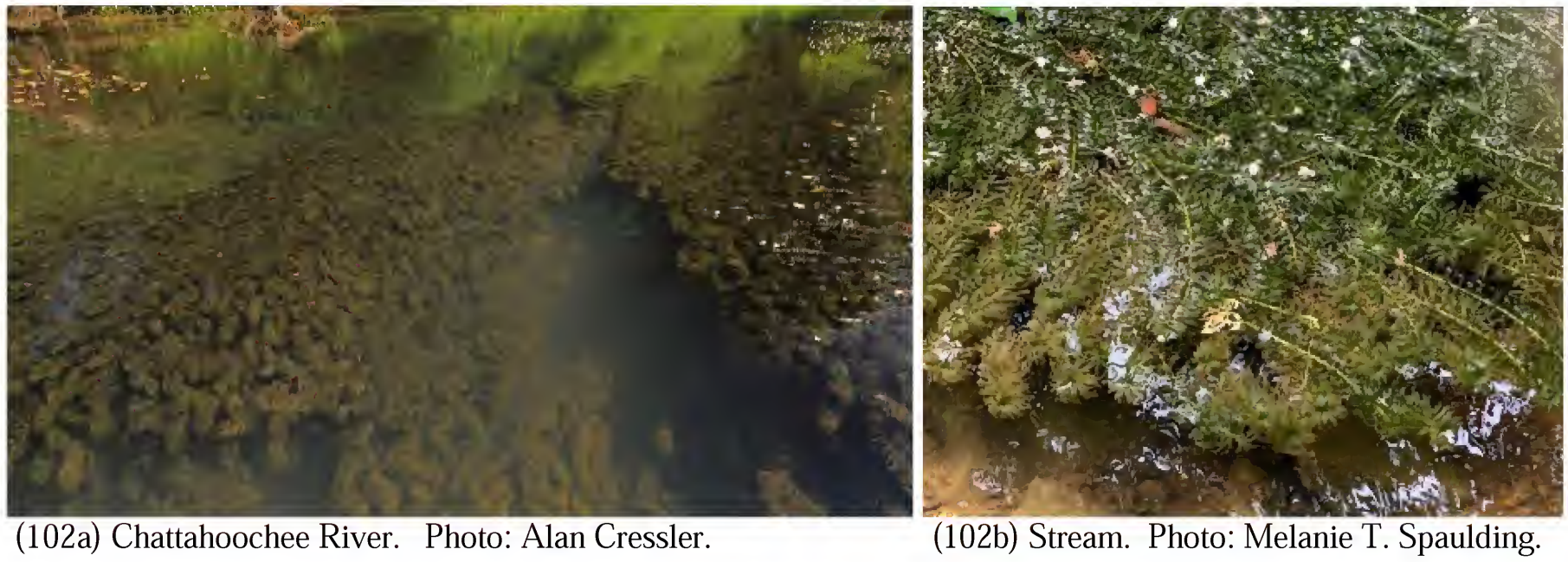


Figure 101. Distribution of *Egeria densa* in northern Alabama.

Brazilian Waterweed, is a noxious pest, able to displace native vegetation (Fig. 102). *Egeria densa* has tendency to clog waterways, impoundments, lagoons, and hydroelectric turbines (Godfrey & Wooten 1979; Yarrow et al. 2007). Populations can grow quickly through stem fragmentation that root readily and develop into new shoots (Haynes 1988). Based on collections reported in the Alabama Plant Atlas (Keener et al. 2019), it appears that *E. densa* was once more common in reservoirs along the Tennessee River in northern Alabama. *Hydrilla verticillata*, a frequent weed in Tennessee River reservoirs, is reported by Mony et al. (2007) to outcompete *E. densa*, which could be a factor in the decline of *Egeria* in northern Alabama.



(102a) Chattahoochee River. Photo: Alan Cressler. (102b) Stream. Photo: Melanie T. Spaulding.

Figure 102. *Egeria densa*. A. Fulton Co., Georgia, 9 Jun 2011. B. Cleburne Co., Alabama, 15 Jun 2019.

Brazilian Waterweed is dioecious, but only male (staminate) plants have been recorded in North America, which suggests that all *Egeria* populations have spread by fragmentation (Haynes 2000a). *Egeria densa* flowers occur on long axillary peduncles projected at or just above the water surface (Haynes 1988). If submersed, the petals close, entrapping air bubbles, keeping the stamens or stigmas dry (Haynes & Holm-Nielsen 2001). The leaves of *Egeria* are only 2-cell-layers thick, a character that enables laboratory experiments to effectively demonstrate cytoplasmic streaming (Haynes 2000a).

Hydrilla can be mistaken for *Egeria* since both genera have whorled leaves. However, *Hydrilla* leaves have sharp teeth along their margins and a spiny midrib beneath, making the plant rough to the touch. Leaves of *Egeria* are finely serrate and lack spines on the midrib, making them smooth to the touch. The leaves *Hydrilla* are also well spaced on older lower stems and crowded near terminal portions, while the leaves of *Egeria* are crowded throughout (Fig. 103).

Figure 103. *Egeria densa* leaves, lake/3-Mile Creek, Mobile Co., Alabama, 15 Apr 2018. Photo: Howard Horne.

2. ELODEA Michaux 1803

[Greek *elodes*, marshy; alluding to their aquatic habitat]

1. Elodea canadensis Michx. {Canadian} — CANADIAN WATERWEED; BROAD WATERWEED; COMMON WATERWEED (Fig. 104). [*Anacharis canadensis* (Michx.) Planch.; *Philotria canadensis* (Michx.) Britt.]

Submersed aquatic, perennial herb. Springs, lakes, streams, and rivers; flowers and fruits July–September; very rare in the Highland Rim and Coastal Plain; rare in the Cumberland Plateau and Ridge & Valley (Fig. 105). Native to Canada and much of the USA; introduced in lakes and waterways of Europe, New Zealand, and Australia, where it is considered an invasive pest (Haynes & Holm-Nielsen 2001).

Figure 104. *Elodea canadensis* from spring in Etowah Co., Alabama, 11 Aug 2018. Photos: Dan Spaulding.

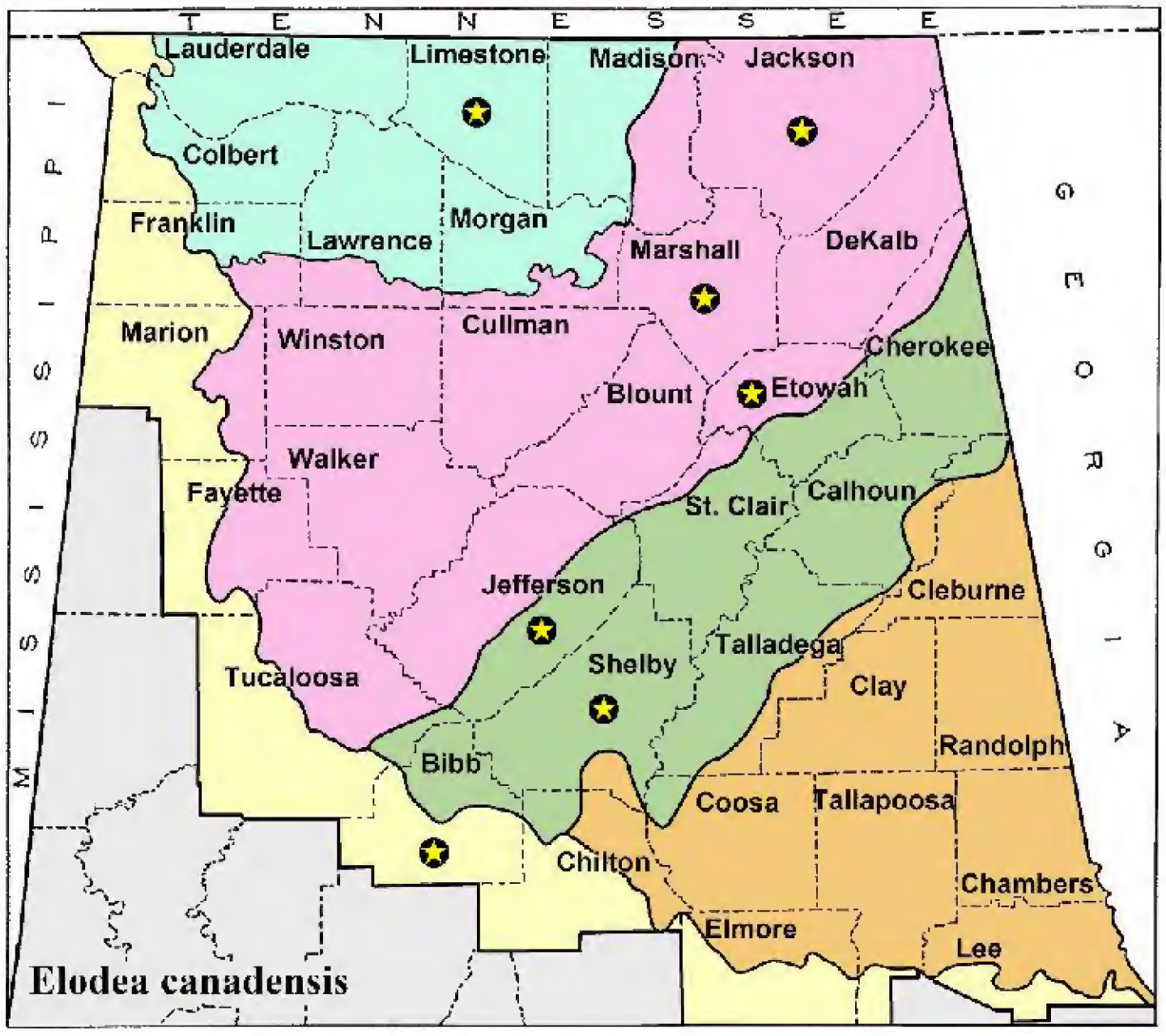


Figure 105. Distribution of *Elodea canadensis* in northern Alabama.

Canadian Waterweed is typically found growing in clear, calcareous waters. It is easily recognized by its finely serrate leaves in whorls of three (Fig. 106). The species is widespread in North America and not known to be weedy within its native range (Haynes 1988). *Elodea canadensis* increases food availability for fish and ducks by providing cover for insects and other small aquatic

organisms (Spicer & Catling 1988). The species is currently listed as critically imperiled (S1) in Alabama (ALNHP 2017) and was considered an endangered species in Alabama by Freeman et al. (1979). A possible factor in its decline is perhaps the deterioration of water quality. Haynes (1980) wrote that it was "rare in the Mobile Delta and in reservoirs of the Tennessee River, the species is probably extirpated from the State." Collections by Mohr (1901) from Baldwin and Mobile counties are historical, but more recent populations have been discovered since Haynes' publication.

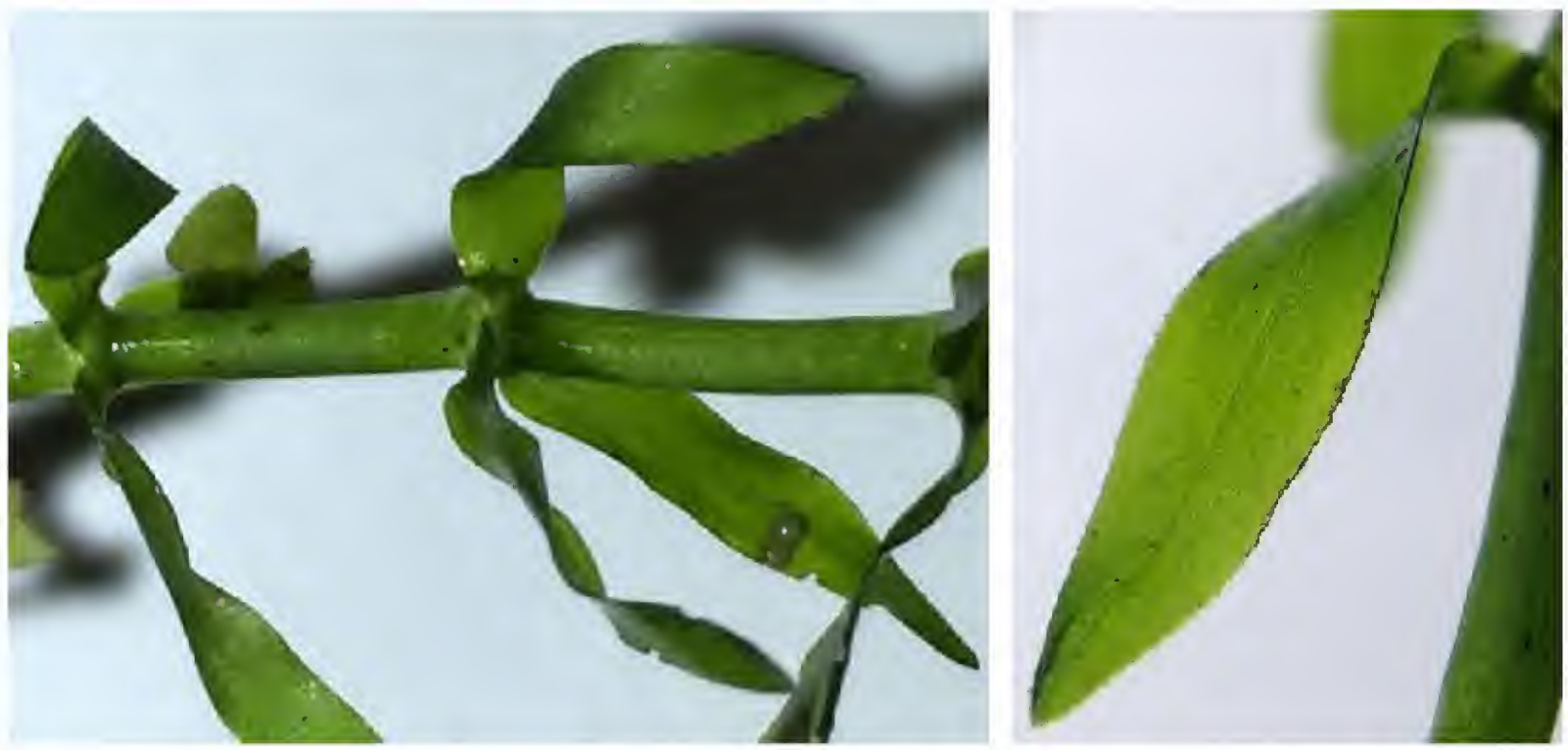


Figure 106. *Elodea canadensis*, close-up of leaves, Etowah Co., Alabama, 11 Aug 2018. Photos: Dan Spaulding.

Elodea canadensis is dioecious, with male (staminate) and female (pistillate) flowers on separate plants. The flowers are elevated at or above water's surface (Fig. 107a) via an elongated floral tube (hypanthium) in female plants or on a lengthened flower stalk (pedicel) in male plants (Haynes & Holm- Nielsen 2001). Staminate flowers release a non-wettable pollen that floats until it contacts a stigma of a pistillate flower (Haynes 1988). This species can also reproduce vegetatively by stem fragmentation. In autumn, the upper stems cease to elongate and the terminal leaves become tightly clustered, forming turions (Fig. 107b) that are capable of growing new plants (Haynes & Holm-Nielsen 2001).

(107a) Flowers on long stalks.

(107b) Turions formed at end of branches.

Figure 107. *Elodea canadensis* A. Yaroslavl region, Russia, 26 Jul 2010. Photo: Eduard Garin. B. Plant with turions (lighter green, clustered shoots) at tips of branches, Maine, USA. Photo: Don Cameron.

Elodea nuttallii (Planch.) St. John [Nuttall's Waterweed] is a similar species reported from Alabama (St. John 1965), but no valid specimens have been observed. It has flexuous, narrow leaves (avg. 1.3 mm long) with pointed tips (Fig. 108), which do not become densely crowded on upper stems (Haines 2011). As in *Elodea canadensis*, the pistillate flowers are on an elongated floral tube, but the staminate flowers of *E. nuttallii* are sessile and later detach from the plant and float up to the water surface. *Elodea canadensis* differs by having firm, broader leaves (avg. 2 mm) with blunt tips, which become crowded and dense in the upper portion of the stem late in season.

Figure 108. *Elodea nuttallii*, Lincoln Co., Maine, 1 Aug 2002. Photos: Don Cameron.

Egeria densa is sometimes confused with *Elodea canadensis*, but leaves of *Egeria* occur in whorls of four or more instead of threes. *Elodea* also has smaller flowers, its petals are 2.5–5 mm long and about the same length as the sepals. *Egeria* flowers are conspicuous, its petals are 8–11 mm long and distinctly exceed the sepals

3. HYDRILLA L.C. Richard 1814
[Greek *hydro*, water; referring to the habitat]

1. Hydrilla verticillata (L.f.) Royle {whorled} — HYDRILLA; WATER-THYME (Fig. 109).

Figure 109. *Hydrilla verticillata*, Mallard Creek, Lawrence Co., Alabama, 19 Aug 2018. Photos: Dan Spaulding.

Submersed aquatic, perennial herb with rhizomes and tubers. Lakes, reservoirs, swamps, marshes, ponds, sluggish streams and rivers; flowers and fruits May–August; frequent in the Highland Rim and Coastal Plain; uncommon in the Cumberland Plateau and Ridge & Valley; rare in the Piedmont (Fig. 110). This species is often locally abundant. It occurs in reservoirs along the Tennessee River and has invaded the Cahaba River and Tallapoosa River. The origin of *Hydrilla* is uncertain, but it is believed to be native to the warmer areas of Asia, where it is widespread (Langeland 1996). *Hydrilla* has become an invasive weed throughout the world in tropical, subtropical, and temperate regions (Haynes & Holm-Nielsen 2001).

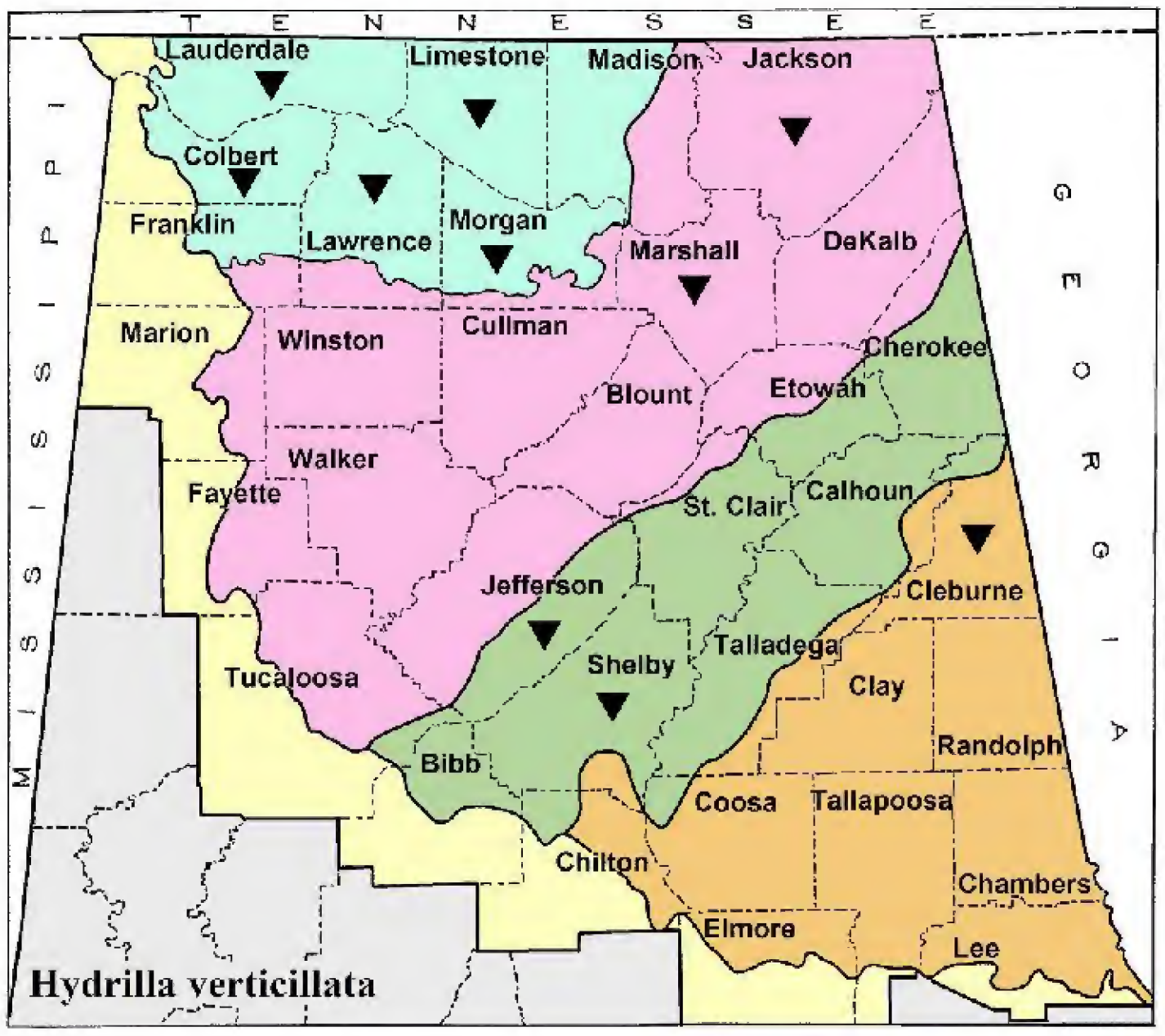
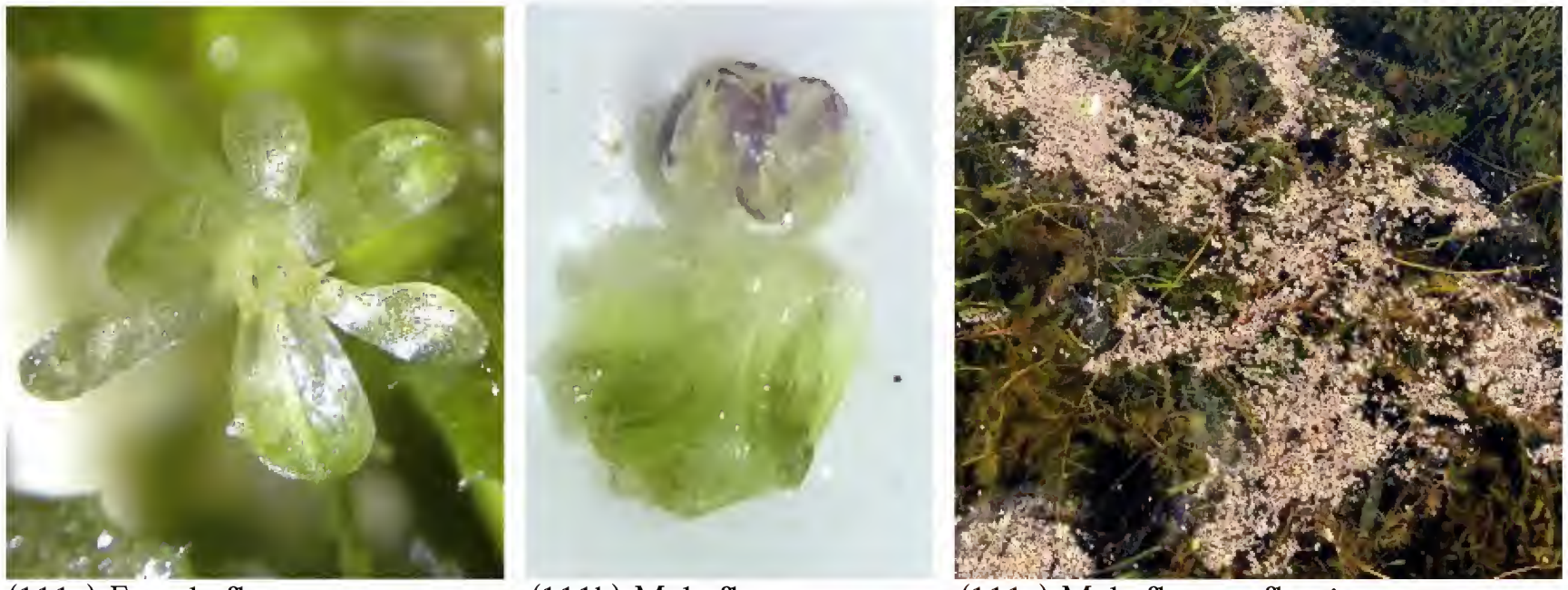


Figure 110. Distribution of *Hydrilla verticillata* in northern Alabama.

Hydrilla was first discovered from Austin, Florida, in 1959. It has since become a noxious pest, spreading rapidly and choking waterways in warmer regions throughout the USA (Haynes & Holm-Nielsen 2001). *Hydrilla* is a monotypic genus with a single variable species that grows in a variety of aquatic habitats in fresh or brackish waters. Plants multiply and spread most rapidly by turions, tubers, and fragmentation of stems, yielding new plants very quickly (Haynes 2000a). Monetary losses can occur when waterfront property values drop or when recreational access is hindered, and water movement for irrigation is impacted. This species is often transported into new locations by vegetative fragments, often when attached to boats and trailers (Haynes 1980). *Hydrilla* management methods include introduction of the grass carp (*Ctenopharyngodon idella*), mechanical removal, and use of herbicides (Langeland 1996). Haynes (1980) documented *Hydrilla* only from Clarke and Choctaw counties (Coffeeville Lake, Tombigbee River), but it has now spread throughout Alabama.

The flowers of *Hydrilla* are unisexual, with staminate (male) and pistillate (female) flowers on separate plants or on the same plant (Haynes 2000a). These two biotypes, dioecious and

monecious, have been documented as occurring in the USA. Only pistillate dioecious plants, however, are known in the USA (Madeira et al. 2000). Both biotypes occur in the large reservoirs along the Tennessee River in northern Alabama (David Webb, pers. comm. 2019). The biotypes can often be distinguished by their growth habit. Pistillate dioecious plants are robust, growing vertically and creating surface mats, whereas the monoecious biotype is more slender and generally forms horizontal mats underwater (Tennessee Flora Committee 2014). The monecious biotype is capable of producing viable seeds (Madeira et al. 2009). Pistillate flowers (Fig. 111c) remain attached to the plant and extend to the water surface by an elongated floral tube. Staminate flowers (Fig. 111b) are released under water and float to the surface, often in large numbers (Fig. 111c). Initially, anthers adhere in "pockets" of each sepal and later the stamens spring forward, "catapulting" their pollen into the air, with most landing in the water but some ultimately landing on stigmas of the female (Haynes & Holm-Nielsen 2001).



(111a) Female flower. (111b) Male flower. (111c) Male flowers floating on water.

Figure 111. *Hydrilla verticillata*. A. Mallard Creek, Lawrence Co., Alabama, 19 Aug 2018. B-C. Guntersville Reservoir/Tennessee River, Marshall Co., Alabama, 8 Oct 2018. Photos: Dan Spaulding.

Egeria densa and *Elodea canadensis* can be confused with *Hydrilla* since both are submersed aquatics with whorled leaves. *Hydrilla* is easily separated by its toothed leaves (Fig. 112a) and by its small spine-like teeth on the midribs underneath (Fig. 112b), which make the plant rough to the touch. Leaves of the other species (*Egeria* and *Elodea*) have finely serrate margins and lack teeth on the midribs, thus are smooth to the touch.

(112a) Conspicuously toothed leaves. (112b) Undersurface of leaves with spine-like teeth.

Figure 112. *Hydrilla verticillata*, Tennessee River, Jackson Co., Alabama, 14 Aug 2018. Photos: Dan Spaulding.

4. **Limnobium** L.C. Richard 1814

[Greek *limnobios*, living in pools; a reference to its habitat]

1. Limnobium spongia (Bosc) L.C. Rich. ex Steud. {a sponge} — AMERICAN FROG'S-BIT; AMERICAN SPONGE-PLANT; NORTH AMERICAN FROGBIT (Fig. 113).

Figure 113. *Limnobium spongia*, Montgomery Co., Alabama, 28 Aug 2015. Photo: Wayne Barger.

Emersed or floating aquatic, perennial herb with stoloniferous stems. Lake margins, sloughs, marshes, swamps, and ponds; flowers and fruits June–September; rare in the Cumberland Plateau; uncommon in the Coastal Plain (Fig. 114). Its native distribution ranges from New Jersey along the Atlantic Coastal Plain south to Florida and west mostly through the Gulf Coastal Plain to east Texas and northward through the Mississippi drainage to southern Illinois (Catling & Dore 1982). Non-persisting, introduced populations have been documented from New York, Connecticut, and northern Indiana (Les & Capers 1999). This species has also been introduced into California, where it has become an invasive weed (Hrusa et al. 2002).

In northern Alabama, *Limnobium spongia* is known only from Guntersville Reservoir (Tennessee River) in the Sequatchie Valley district of the Cumberland Plateau. It was first discovered in 2015 by David Webb in Marshall County and again in 2018 from Jackson County (David Webb, pers. comm. 2019). Intensive field work of aquatic environments by Haynes (1980) and a floristic survey of the Guntersville Reservoir in the 1990's (Spaulding 1999) failed to document this species from the northern regions of the state. *Limnobium* is likely to have been introduced recently in northern Alabama (David Webb, pers. comm. 2019) and could potentially spread to other reservoirs of the Tennessee River system. The dispersal of *Limnobium* in the USA is believed to be by natural agents, not by horticultural introductions (Lowden 1992). The seeds are likely dispersed by various duck species, which are known to consume the fruit (Les & Capers 1999).

Although American Frog's-Bit is indigenous to North America, it has the potential to become weedy in certain regions of its range (Les & Capers 1999). *Limnobium spongia* usually forms dense mats from stoloniferous stems that are floating or suspended just below water surface (Fig. 115), but

plants can also be stranded during low water. Populations are free-floating (Fig. 116a) or rooted at the nodes of its stolons in shallow water or on mudflats. The floating leaves have short petioles and a leaf blade with a central disc of inflated, spongy cells (aerenchyma) underneath (Fig. 116b). The emersed leaves have longer petioles and these leaf blades lack a central spongy area (Lowden 1992). The two leaf types are frequently found on the same plant (Haynes 2000a).

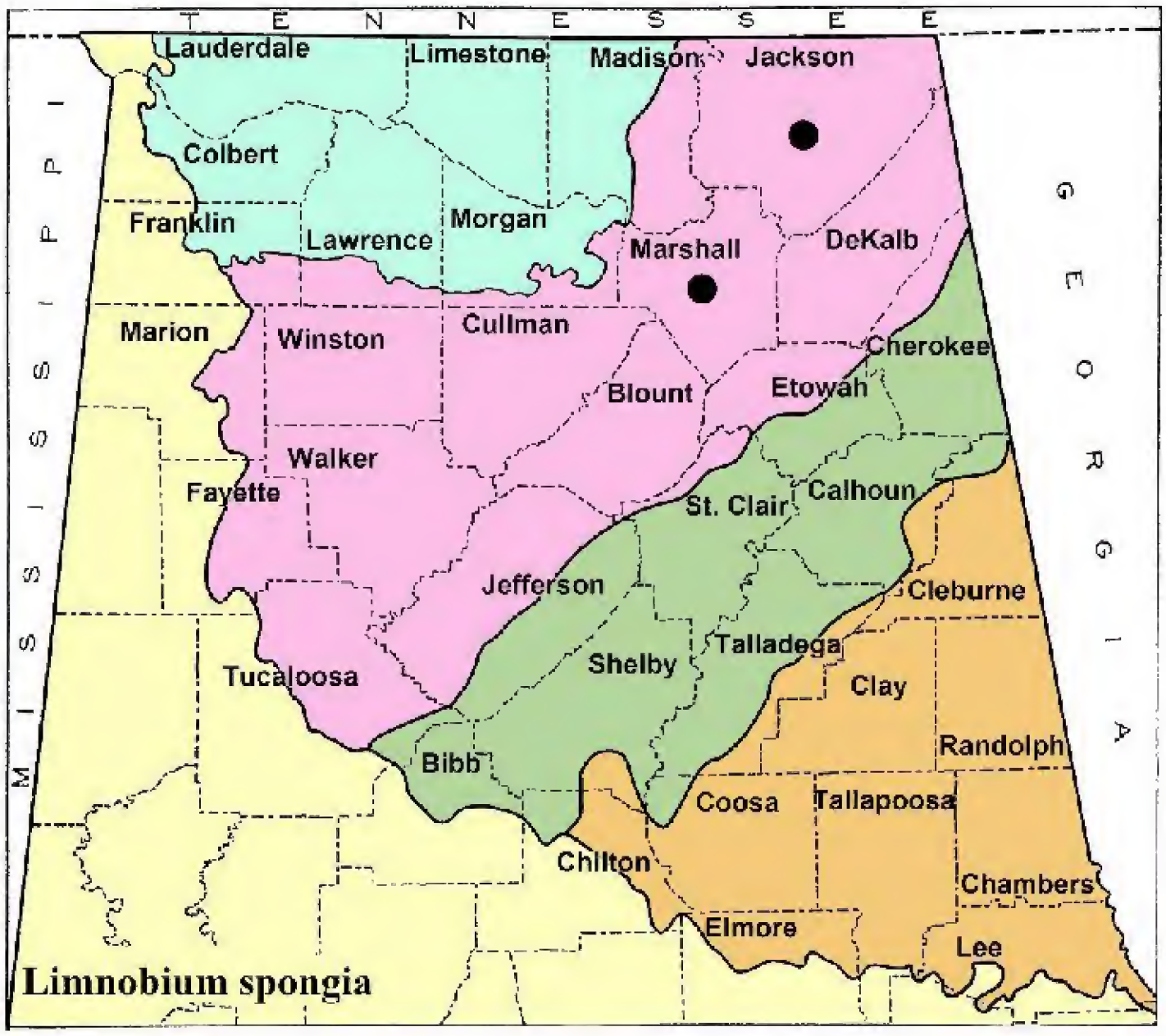


Figure 114. Distribution of *Limnobium spongia* in northern Alabama.

Figure 115. *Limnobium spongia*, reservoir margin, Marshall Co., Alabama, 23 Sept 2015. Photo: David Webb.

(116a) Free floating form.

(116b) Spongy disc on underside of floating leaves.

Figure 116. *Limnobium spongia*, St. Johns County, Florida, 18 Mar 2019. Photos: Eric M. Powell.

Spongeplant is monoecious — it has unisexual flowers (male & female) on the same plant (Fig. 113). It is principally wind pollinated (anemophily), but aphids (Aphididae) and their predators, ladybird beetles (Coccinellidae), are often present on the floral parts during anthesis (Lowden 1992). Flowering occurs primarily on rooted plants with emersed leaves. Following pollination, fruiting stalks curve downward (Fig. 117a–b), with fruit usually forming under water (Haynes 2000a).

Figure 117. *Limnobium spongia* with fruits, Marshall Co., Alabama, 14 Oct 2015. Photos: David Webb

5. **NAJAS** Linnaeus 1753

[Greek, *Naias*, a water-nymph; a reference to their aquatic habitat]

Hydrocharitaceae has some of the most specialized pollination mechanisms found within the angiosperms, and *Najas* is the only freshwater genus in the family with subsurface, hydrophilous pollination (Les et al. 2010). In submerged hydrophily, pollen grains are released underwater from male flowers, sink and attach to the stigmas of female flowers (Cox 1988). Molecular data show that *Najas* is most likely closely related to a clade that includes the genera *Hydrilla* and *Vallisneria* (Tanaka et al. 1997; Chen et al. 2012).

1. Leaf blades with conspicuous spinulose teeth along margins; leaves stiff and recurved with age; terminal internodes becoming shorter, therefore leaves are tufted at top, giving plant a bushy habit; areolae (cell-like pits) of seed coat in ladder-like rows (seen in mature fruit).....**3. Najas minor**
1. Leaf blades with small, inconspicuous teeth along margins; leaves flaccid, mostly straight: terminal internodes about equal in different parts, therefore plant not tufted at top; areolae of seed coat not in ladder-like rows (best observed in dried mature fruit).

    2. Leaves filiform, 0.1–0.3 mm wide with a gradually tapering apex and an abruptly expanded base; leaf margins with 13–17 multicellular teeth > 0.5 mm long; leaf sheaths with truncate or auriculate shoulders; areolae longer than broad.....**1. Najas gracillima**
    2. Leaves linear, 0.5–1.4 mm wide with an abruptly tapering apex and a gradually expanded base; leaf margins with 50–100 minute unicellular teeth per side < 0.5 mm long; leaf sheaths with sloping or rounded shoulders; areolae of seeds about as long as broad...**2. Najas guadalupensis**

1. Najas gracillima (A. Braun ex Engelm.) Magnus {very slender} — SLENDER WATER-NYMPH; THREAD-LIKE NAIAD; SLENDER NAIAD (Fig. 118).

Figure 118. *Najas gracillima*, from karst pond near Sgonico, Italy (Friuli region), 30 Sep 2008. Photos: Alexander Mrkvicka. <http://flora.nhm-wien.ac.at >

Submersed aquatic, annual herb. Lakes; flowers and fruits July–October; very rare in the Piedmont (Fig. 119). This species is native to Eurasia and the eastern half of North America. Populations are scattered from Ontario to Newfoundland, south through Minnesota and Maine, to Alabama and Mississippi; disjunct in California. Through genetic studies, Les et al. (2013) concluded that *Najas gracillima* was introduced into California from Asian material, and it is potentially invasive on the West Coast. In eastern North America, however, it is indigenous and imperiled.

Fernald (1923) stated that *Najas gracillima* "is one of the most distinct species of the genus on account of its straight linear-setaceous leaf-blades strongly divergent from the conspicuously auricled and scarious sheathing base and its commonly subfalcate, very slender fruits with about 24 rows of longitudinal elongate areolae." *Najas gracillima* looks somewhat like *N. minor*, but Slender Water-Nymph has flexible, mostly straight leaves with small teeth along its margins (Fig. 120a), and areolae on the seed coat are longer than broad (Fig. 120b). *Najas minor* has stiff, distinctly curved

leaves with conspicuous teeth along the margins (when mature), and areolae on the seed coat are broader than long (transversely elongate) in ladder-like rows.

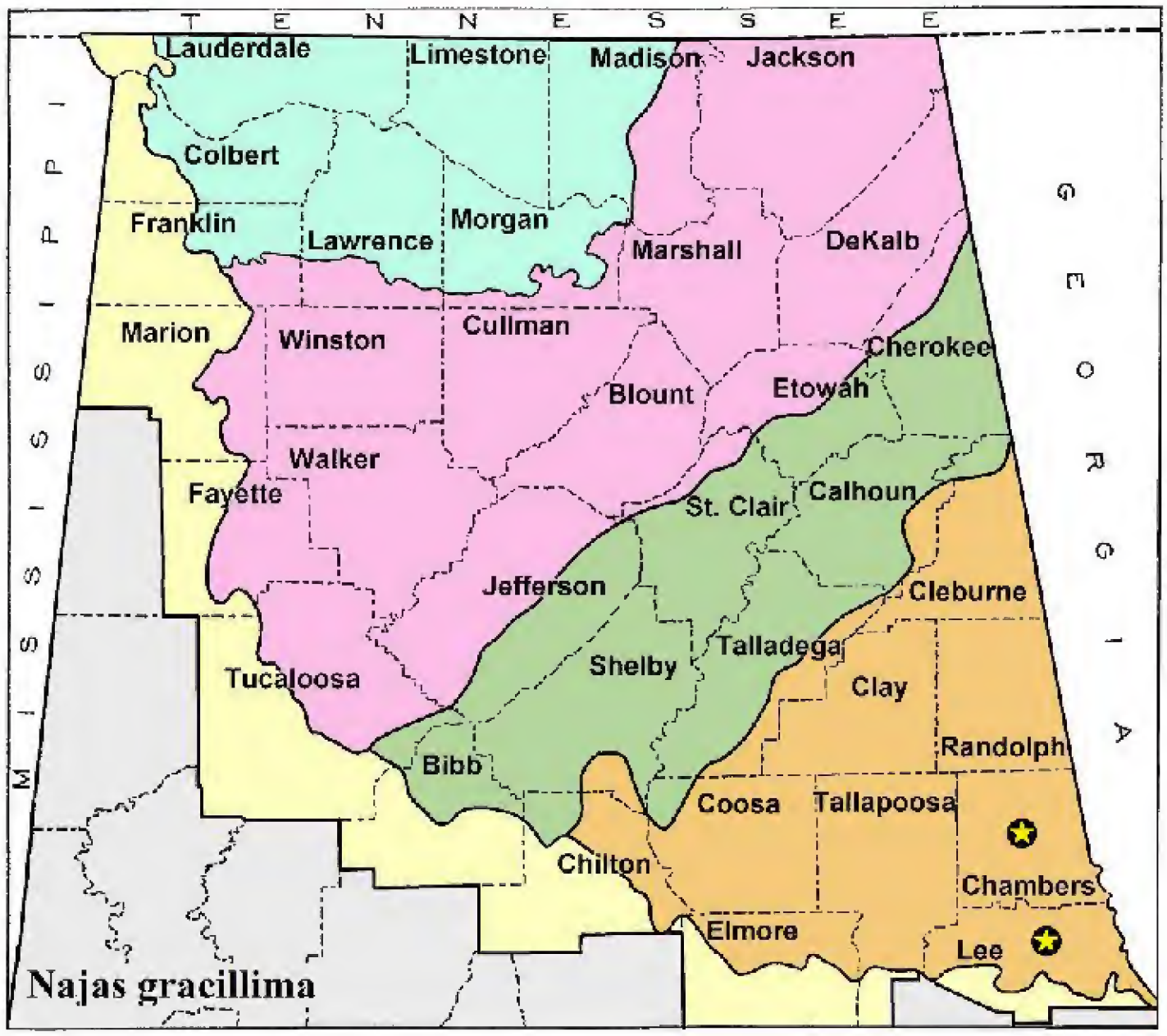


Figure 119. Distribution of *Najas gracillima* in northern Alabama.

(120a) Leaves with small multicellular teeth. (120b) Areolae longer than broad.

Figure 120. *Najas gracillima.* A–B. UNA, *Myhre 7219*, Benfield Lake, Carlton Co., Minnesota, 17 Aug 1997. Photos: Dan Spaulding.

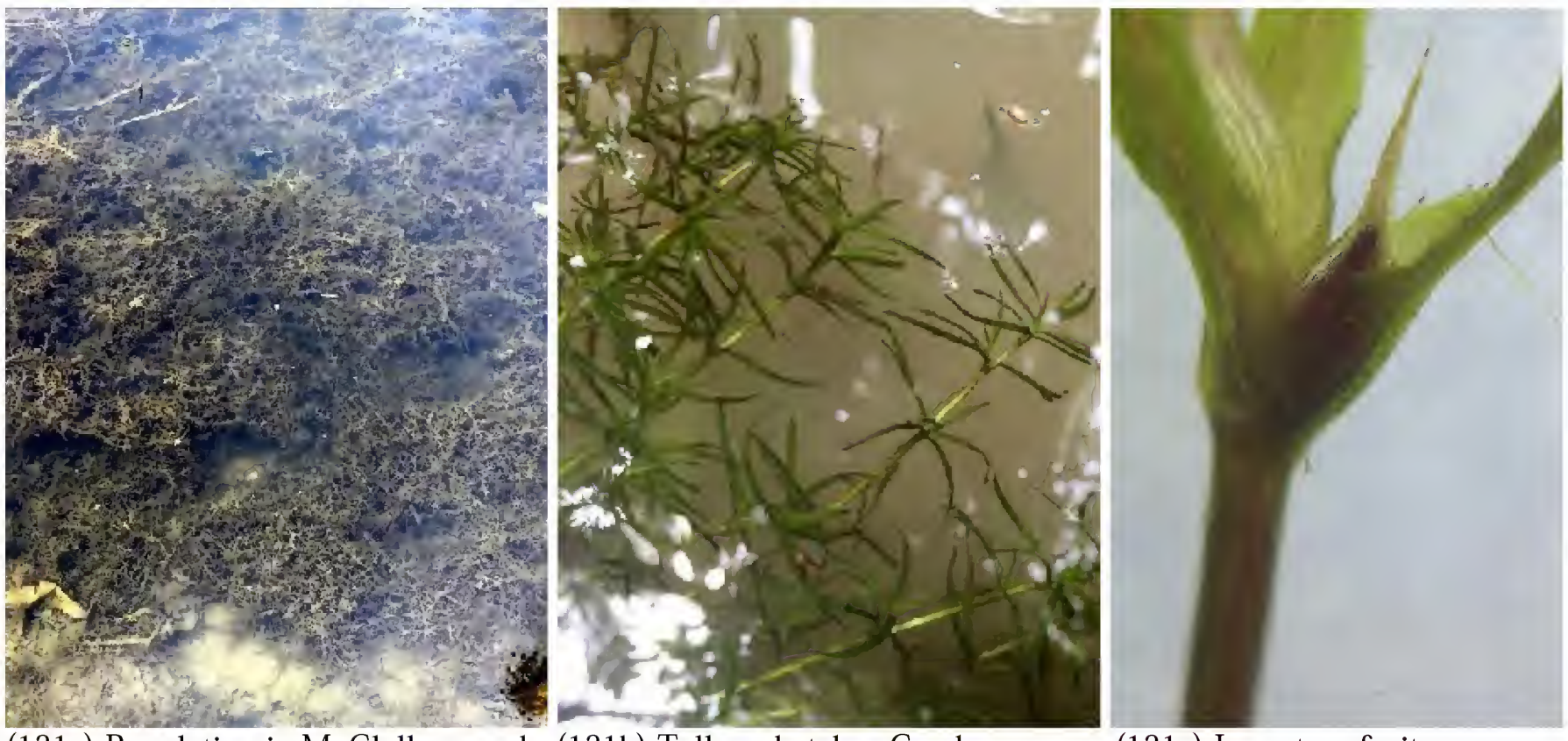
Najas gracillima was first discovered in Alabama by Lovett E. Williams in the Piedmont of Lee County on July 5, 1958. Williams collected the plant in Lake Ogletree, just south of Auburn, where it was apparently abundant in 2 feet of water. He deposited his collection at Florida State University Herbarium (FSU) but did not identify it to species. The FSU herbarium specimen was

examined and annotated to *N. gracillima* in 1974 by Robert Haynes and W. Alan Wentz (1974), students at Ohio State University. The population at Lake Ogletree was never visited by Haynes (Robert Haynes, pers. comm. 2019).

On July 2, 1979, Haynes discovered another population of *Najas gracillima* in the Piedmont in Lafayette City Lake in Chambers County, Alabama. He recorded it as being abundant in water to about 3 feet deep. In 1983, during a later visit to this public fishing lake, he noted *N. gracillima* was now rare, found only in hollow stumps, apparently protected from marauding grass carp (*Ctenopharyngodon idella*). Unfortunately, this population is now believed to be extirpated because of the introduction of this fish species (Robert Haynes, pers. comm. 2018). Studies on grass carp reveal that they prefer *Najas* to other aquatic plants (Wiley et al. 1986). *Najas gracillima* has been erroneously reported for Barbour and Cleburne counties (SERNEC 2018) — duplicates of these specimens have been annotated to *N. guadalupensis* by Haynes.

Najas gracillima thrives in clear, clean waters and is intolerant of pollution (Haynes 1977). It has disappeared or been reduced in abundance throughout much of its range due to the degradation of water quality (Wentz & Stuckey 1971). Conversely, *Najas minor*, more tolerant of eutrophic waters, has become abundant and widespread. The Alabama Natural Heritage Program (2017) lists *Najas gracillima* as critically imperiled (S1).

2. Najas guadalupensis (Spreng.) Magnus var. **guadalupensis** {of the Island of Guadalupe} — SOUTHERN WATER-NYMPH; COMMON WATER-NYMPH; SOUTHERN NAIAD; GUADALUPE WATER-NYMPH (Fig. 121a–c).



(121a) Population in McClellan pond. (121b) Tallaseehatchee Creek. (121c) Immature fruit.

Figure 121. *Najas guadalupensis*. A. Calhoun Co., Alabama, 21 Jun 2018. B. Calhoun Co., Alabama, 23 May 2018. C. South Branch Cane Creek, Calhoun Co., Alabama, 22 May 2018. Photos: Dan Spaulding.

Submersed aquatic, annual herb. Lakes, ponds, impoundments, rivers, and streams; flowers and fruits May–October; frequent in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Coastal Plain; uncommon in the Piedmont (Fig. 122). Native to portions of southern Canada and widely distributed throughout the USA (except in Rocky Mountain States) ranging south to the West Indies, Mexico, Central America, and South America (Haynes 2000b).

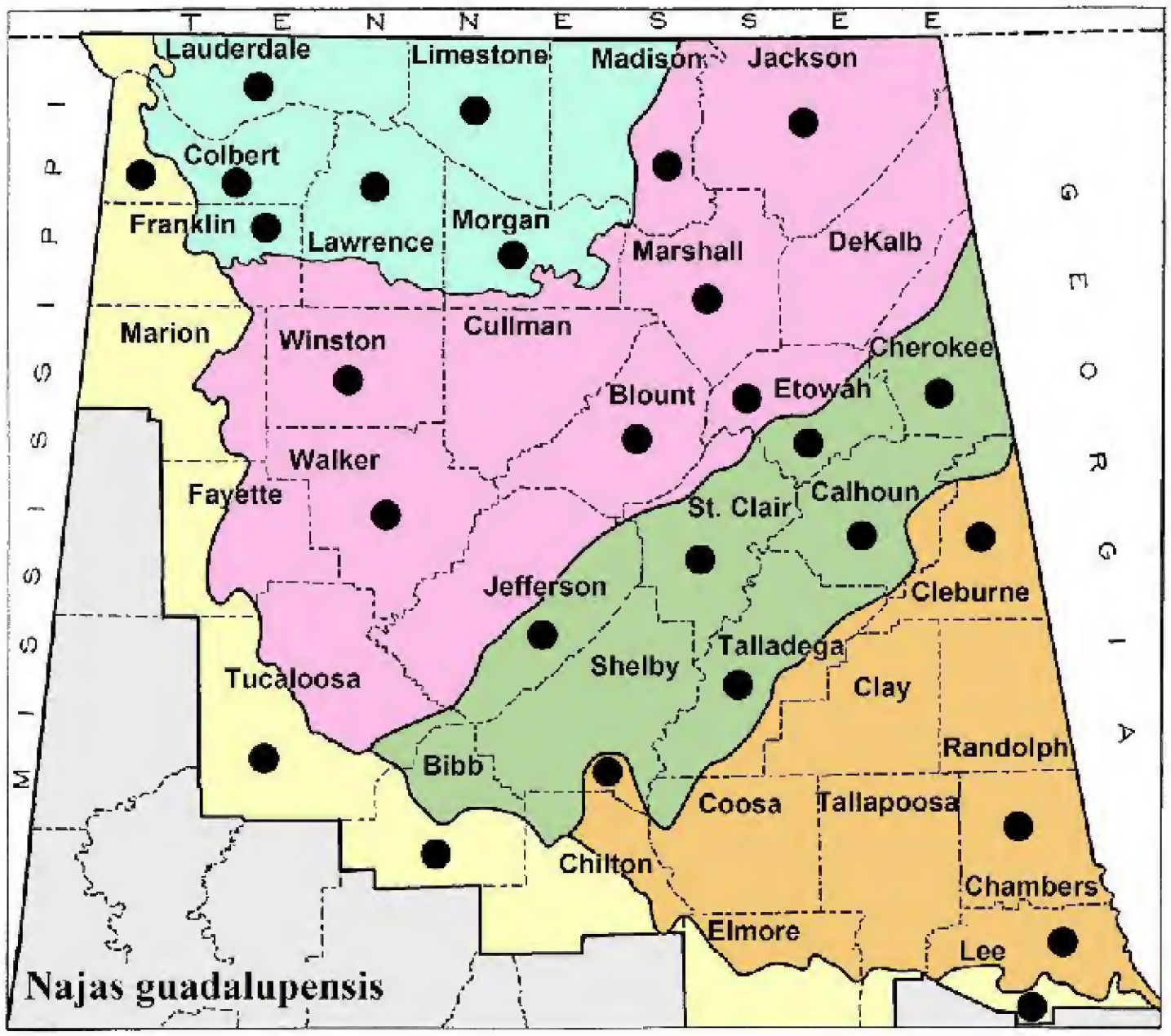
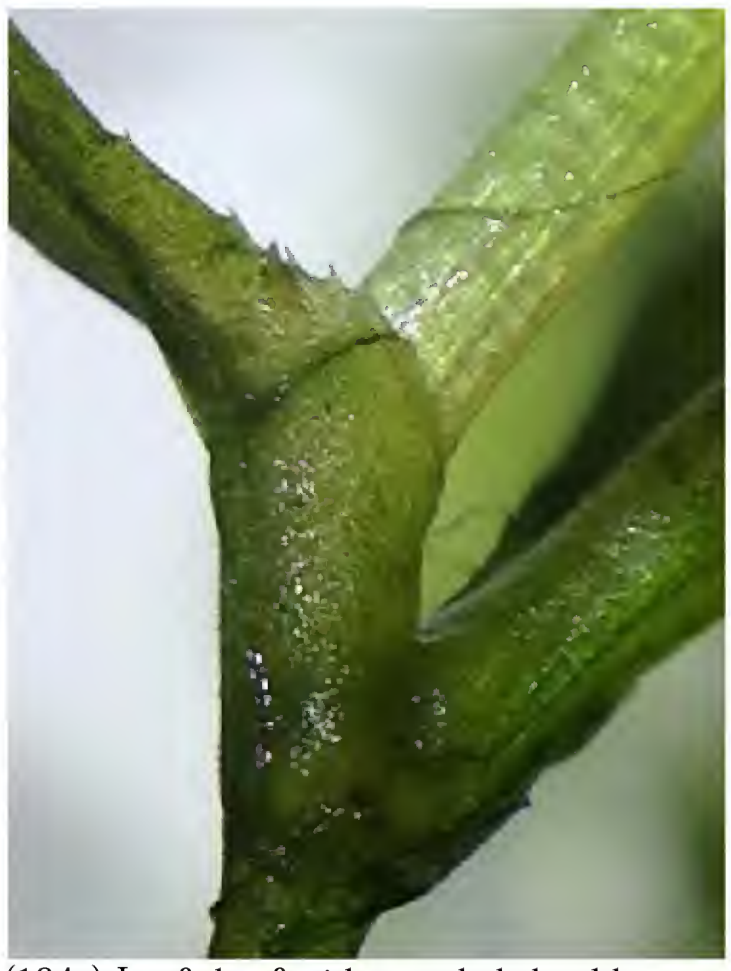


Figure 122. Distribution of *Najas guadalupensis* in northern Alabama.

Najas guadalupensis is a highly variable taxon and has been separated into several varieties or subspecies (Haynes 2000b). Only *N. guadalupensis* var. *guadalupensis* occurs in northern Alabama. *Najas guadalupensis* var. *floridana* is found in rivers, streams, and ponds throughout Florida and in portions of southern Georgia and Alabama (Haynes 2000b). It differs from the typical variety by having 1-locular anthers and leaf blades with 18–42 teeth per side that are often evident to the naked eye. *Najas guadalupensis* var. *guadalupensis* has 4-locular anthers and its leaf blades have 50–100 minute teeth per side (Fig. 123), barely visible to the unaided eye (Haynes 1979).

Figure 123. *Najas guadalupensis* leaves, Calhoun Co., Alabama, 22 May 2018. Photos: Dan Spaulding.

The leaf sheath of Southern Water-Nymph has distinctly rounded, sloping shoulders (Fig. 124a). Its single-seeded fruits are fusiform and the areolae (cell-like pits) of seed coat are about as long as wide (Fig. 124b). *Najas guadalupensis*, like most naiads, is highly fertile and produces a lot of fruits (Meriläinen 1968). The seeds are an important food source for waterfowl and a favorite food of eastern ducks, which eat every part of the plant (Martin et al. 1951).



(124a) Leaf sheaf with rounded shoulders.

(124b) Areolae of seed coat about as long as broad.

Figure 124. *Najas guadalupensis*. A. Valley Creek, Jefferson Co., Alabama, 31 Jul 2018. B. AMAL, *Keener 4919*, pond in St. Clair Co., Alabama, 28 Sep 2008. Photos: Dan Spaulding.

3. Najas minor All. {smaller} — BRITTLE WATER-NYMPH; BRITTLE NAIAD; SPINY-LEAF NAIAD; BRITTLE-LEAF NAIAD (Fig. 125a–c).

(125a) Population in lake.

(125b) Toothed, curved leaves.

(125c) Immature fruit.

Figure 125. *Najas minor*. A. Cherokee Co., Alabama, 22 Aug 2018. B–C. Lafayette City Lake, Chambers Co., Alabama, 30 Jul 2018. Photos: Dan Spaulding.

Submersed aquatic, annual herb. Ponds, lakes, impoundments, marshes, swamps, and sluggish rivers; flowers and fruits July–October; frequent in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Coastal Plain; uncommon in the Piedmont (Fig. 126). Native to Europe, Asia, and North Africa; introduced in the USA (Haynes 2000b).

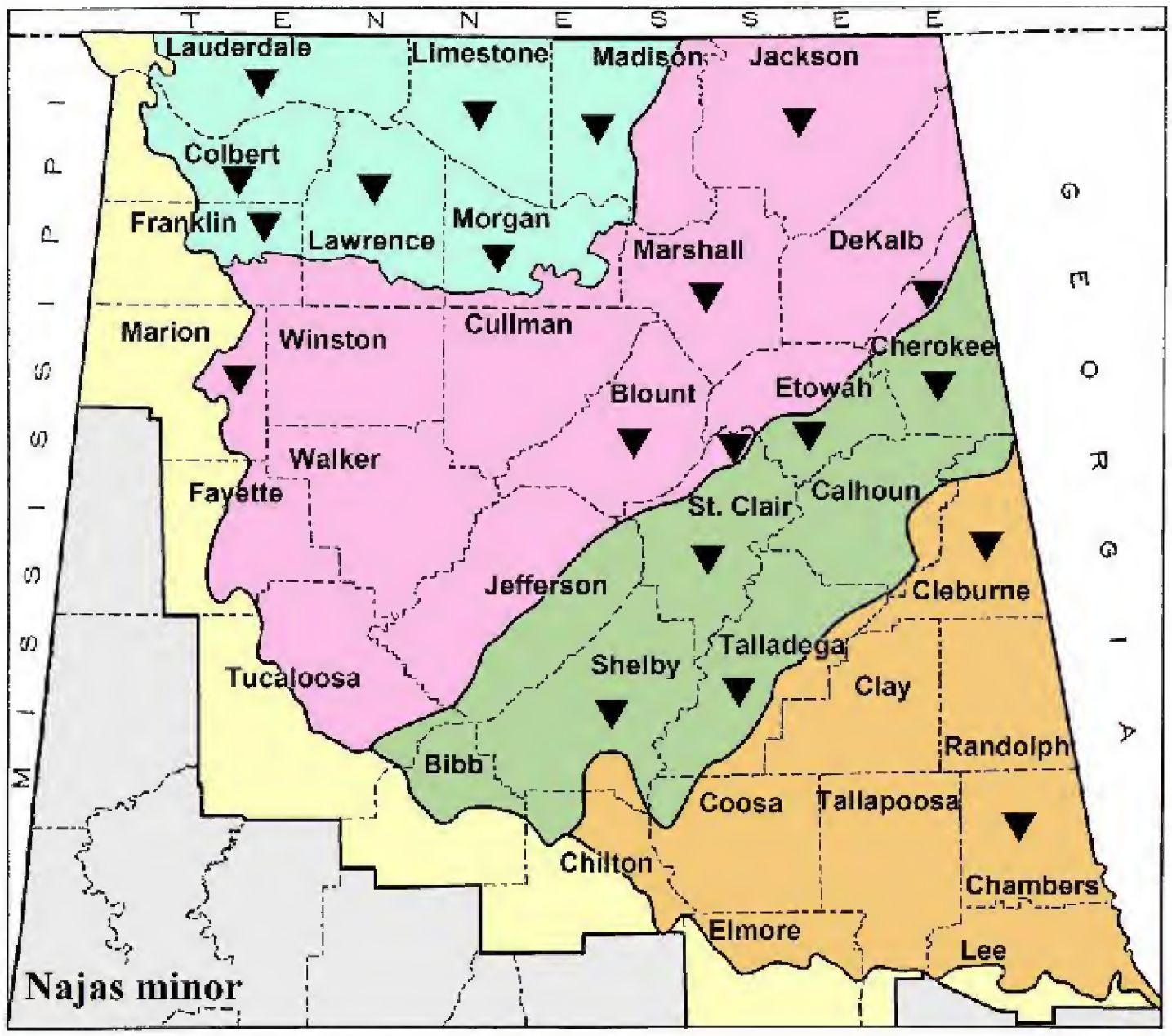


Figure 126. Distribution of *Najas minor* in northern Alabama.

This species invaded North America over 80 years ago. It was first collected in 1932 by Lawrence E. Hicks in 1932 from Lake Cardinal in Ohio, then again by R.T. Clausen in 1934 from the Hudson River in New York (Wentz & Stuckey 1971). *Najas minor* has become widespread in eastern North America but also occurs in California and Washington State (Kartesz 2018). It can thrive in eutrophic to somewhat polluted waters and is likely dispersed in North America by waterfowl that relish its fruits (Meriläinen 1968). *Najas minor* grows in the shallows of lakes, ponds, and large, sluggish rivers with muddy or silty bottoms. In northern Alabama, Brittle Water-Nymph has become a common aggressive weed in reservoirs along the Tennessee River.

As an annual, Brittle Water-Nymph requires seed development for reproduction. It is monoecious, with solitary, unisexual flowers developing within the leaf axils of the same plant, with staminate (male) flowers produced mostly above the pistillate (female) flower. Pollination occurs completely underwater. Male flowers release pollen grains that slowly sink, with some making contact with a stigma of the female flower, enabling pollination (Haynes 1988).

Najas minor is one of the more distinctive species of the genus because of its tufted, curved leaves with conspicuous teeth along the margins (Fig. 127a). The leaves of *N. gracillima* are straight, very narrow, with smaller, less noticeable teeth. Wentz and Stuckey (1971) note that "*N. minor* superficially resembles *N. gracillima* in early growth stages, and the often-mentioned recurved-leaf

character of *N. minor* usually does not appear until late in the growing season." The teeth of *Najas minor* are also not as conspicuous on younger leaves.

Mature fruits of *Najas* can help to separate the various species. Those of *Najas minor* have seed coat areolae (cell-like pits) that are transversely elongate (broader than long) and arranged in ladder-like rows (Fig. 127b). Those of *Najas gracillima* have seed coat areolae that are longitudinally elongate (longer than broad) and arranged in offset rows (Haynes 2000b). Characteristics of the seed coat of *Najas* are conspicuous and visible through their transparent fruit wall but are best observed on dried specimens (Meriläinen 1968). Furthermore, the style of *N. minor* is located at the center of fruit apex, while the style of *N. gracillima* is slightly offset to one side.

(127a) Leaves with conspicuous teeth. (127b) Areolae broader than long; fruit curved.

Figure 127. *Najas minor*. A–B. AMAL, *Spaulding 15684*, Marion Co., Alabama, 8 Sep 2018. Photos: Dan Spaulding.

6. **VALLISNERIA** Linnaeus 1753

[Named after Antonio Vallisneri, 1661–1730, an Italian botanist]

1. Vallisneria americana Michx. {American} — AMERICAN EELGRASS; TAPEGRASS; WATER-CELERY; WILD-CELERY (Fig. 128). [*Vallisneria spiralis* auct. non L.]

Figure 128. *Vallisneria americana,* Jackson Co., Alabama, 11 Aug 2018. Photos: Dan Spaulding.

Submersed aquatic, perennial herb with rhizomes. Rivers, lakes, streams, and ponds, as well as brackish bays and estuaries on the coast; flowers and fruits late May–October; frequent in the Highland Rim; uncommon in the Cumberland Plateau and Coastal Plain; rare in the Ridge & Valley; very rare in the Piedmont (Fig. 129). Native to Canada and USA, south through Mexico to Venezuela; also in Asia and Australia (Haynes & Holm-Nielsen 2001). In North America, *Vallisneria americana* occurs primarily east of the Rocky Mountains but grows sporadically in West Coast states and British Columbia (Kartesz 2018).

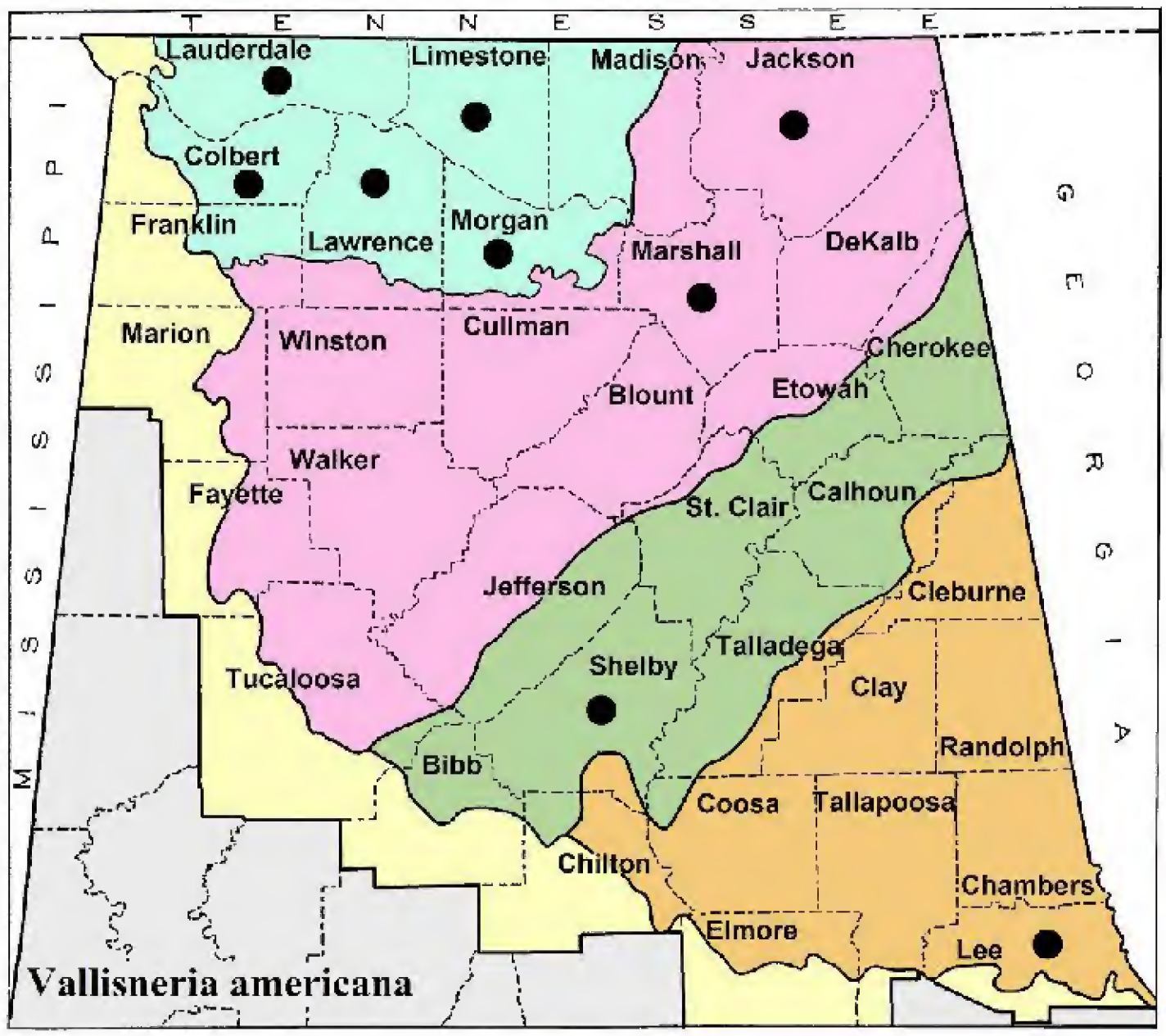


Figure 129. Distribution of *Vallisneria americana* in northern Alabama.

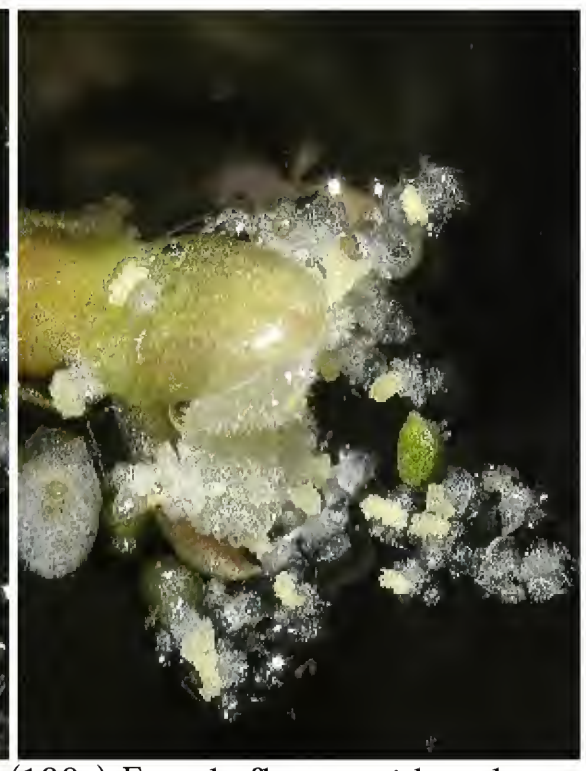
In northern Alabama, American Eelgrass is abundant in larger reservoirs along the Tennessee River and has become a nuisance plant that is being managed with herbicides in areas with developed shoreline (David Webb pers. comm. 2019). *Vallisneria americana* has also been documented in portions of the Cahaba River and from Auburn fishery ponds, where it was likely introduced. Nearly all populations on the Coastal Plain are from Baldwin and Mobile counties (Keener et al. 2019). An Old World species, *Vallisneria spiralis* L. [European Eelgrass], is distinct from *V. americana* but the name has been misapplied in the past to our species (Fernald 1918).

Vallisneria americana is dioecious, with unisexual flowers occurring on separate plants. Haynes & Holm-Nielsen (2001) described the elaborate pollination mechanism. The staminate (male) flowers are tightly packed in a spathe, which is a pouch-like inflorescence attached underwater to the base of the plant by a short stalk (Fig. 130a). At maturity, the valves of the floral spathe separate, releasing numerous unopened staminate flowers that rise to the surface (Fig. 130b). The differences in air pressure outside and inside the flower causes the spathe to open, with the sepals becoming reflexed, forming a floating "boat-like" structure. Staminate flowers drift along the water surface, with some making contact with pistillate (female) flowers (Fig. 130c), which are borne singly

on a long flower stalk (Fig. 131a–c). After pollination the pistillate flower stalk recoils, pulling the fruit underwater where it matures (Fig. 132a). American Eelgrass populations are connected by rhizomes (Fig. 132b) buried in the mud, and when fragments break free, they can produce new colonies.

(130a) Staminate spathes.

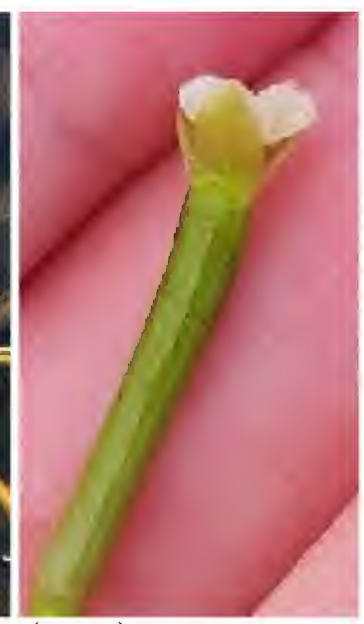
(130b) Floating raft of male flowers.



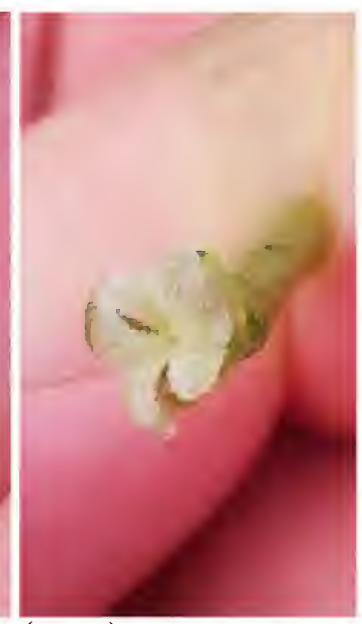
(130c) Female flower with males.

Figure 130. *Vallisneria americana.* A. Staminate inflorescences, opened and unopened. Photo: Don Cameron. B–C. Schuyler Co., New York, 17 Aug 2005. Photos: ©Kevin C. Nixon. < http://www.plantsystematics.org/>

(131a) Pistilate flowers on long stalks.



(131b) Floral tube.



(131c) Female flower.

Figure 131. *Vallisneria americana.* A. Ontario, Canada, 14 Aug 2018. Photo: Liv Monck-Whipp. B-C. New Brunswick, Canada, 6 Aug 2018. Photos: Kitty Maurey.

Sterile plants of *Vallisneria americana* are often confused with immature *Sparganium americanum* Nutt. [American Burr-Reed]. Both species have long linear leaves in basal rosettes, but when *Sparganium* is completely underwater they look extremely similar because the leaves are long and flaccid (Fig. 133). *Vallisneria* can be distinguished by its more flattened leaf base, leaves without a raised midvein, and leaf blades with bands of lacunae (air spaces), which appear as lighter colored wavy lines (Fig. 128). *Vallisneria* also has minute scattered teeth along margin of its leaves and *Sparganium* has smooth margins (Haynes 2000).

Vallisneria neotropicalis Vict. [Large Eel-Grass], is a similar species but has wider leaves often suffused with red and is found mostly in warmer waters of Florida and Cuba (Long & Lakela 1971). Large Eel-Grass has been documented from brackish waters on the coast of Alabama, but

reports (Haynes 1980) of *Vallisneria neotropicalis* from the Cahaba River in Shelby County are in error. This species has occasionally been placed in synonymy with *V. americana* (Godfrey & Wooten 1979; Haynes 2000a; Lowden 1982). However, Les et al. (2008) showed via molecular research that the two are genetically distinct and that "*V. neotropicalis* is not simply a larger growth form of *V. americana,* resulting from a prolonged growing season in more southern latitudes."

(132a) Fruits underwater with coiled stalks.

(132b) Rhizomes (horizontal stems) connecting plants.

Figure 132. *Vallisneria americana.* A. Portage Co., Ohio, 11 Sep 2018. Photo: Mark Warman. B. Tennessee River, Marshall Co., Alabama, 8 Oct 2018. Photo: Dan Spaulding.

Figure 133. *Sparganium americanum*, Cleburne Co., Alabama, 18 Aug 2018. Photos: Dan Spaulding.

Vallisneria americana is valued commercially and is sold in aquarium trade. It has the potential of becoming a noxious weed due to its widespread cultivation (Les et al. 2008). It is an important food source for many waterfowl species. The Canvasback (*Aythya valisineria*), a diving duck species, makes extensive use of the plant as food source, which is reflected in its scientific name (Martin et al. 1951). The common names "tapegrass" and "eelgrass" refer to its long, narrow leaves (Shosteck 1974), and "celery" may allude to the edibility of the plant for wildlife.

FAMILY 6. POTAMOGETONACEAE (Pondweed Family)

Zannichellia had historically been included within its own family, Zannichelliaceae (Haynes & Holm-Nielsen 1987). Its distinction from other aquatic monocot families was based on its sac-like reproductive structures, which envelop the inflorescence (Les & Haynes 1995; Lindqvist et al. 2006). However, various molecular markers suggest that *Zannichellia* has a closer relationship to the Potamogetonaceae (Les & Haynes 1995; Lindqvist et al. 2006; Les & Tippery 2013).

The association between *Zannichellia* and Potamogetonaceae is still somewhat unclear. Some studies show either a sister relationship exist between the two (Petersen et al. 2006; Iles et al. 2009; Les & Tippery 2013) or that *Zannichellia* is embedded within Potamogetonaceae (Les et al. 1997; Lindqvist et al. 2006). Most authors merge Zannichelliaceae into Potamogetonaceae (Stevens 2001; Trias-Blasi et al. 2015; Weakley 2015; APG 2016; Kartesz 2018; Soltis et al. 2018), while Reveal (2012) opted to maintain it as a separate family.

1. Leaves opposite or in pseudo-whorls (appearing whorled because smaller leaves in axils are sometimes elongated); plants entirely submersed; inflorescence axillary, sessile, usually consisting of two unisexual flowers; perianth absent; staminate flowers with 1 stamen, pistillate flowers with cone-like stigmas; fruits oblong-linear, often on a short stalk (stipitate), usually curved and with a persistent beak-like style, 1–2 mm long ..... **3. Zannichellia**
1. Leaves alternate; plants submersed with or without some floating leaves; inflorescence an axillary or terminal spike on a short or long peduncle with whorls of bisexual flowers; perianth consisting of 4 short-clawed sepaloid segments; flowers with 4 stamens and slender or capitate stigmas; fruits ovate, obovate, obovoid or suborbicular, usually oblique with a short beak < 1 mm long (or 2–3 mm long in *Potamogeton crispus*).

    2. Leaves all submersed; leaf blades linear, opaque, stiff, septate, channeled, and turgid; peduncle of inflorescence flexible, flowering spikes borne below or on surface of water; stipules fused to leaf bases forming long leaf sheaths, 10–30 mm long ..... **2. Stuckenia**
    2. Leaves submersed or submersed and floating; submersed leaf blades linear to broader, translucent, flexible, and flat; peduncle of inflorescence stiff, flowering spikes elevated above the water surface or submersed; stipules of submersed leaves free in axils of leaves or fused with leaf bases to form short leaf sheaths, less than 10 mm long ..... **1. Potamogeton**

1. POTAMOGETON Linnaeus 1753

[Greek *potamos*, river, and *geton*, neighbor; alluding to their aquatic habitat]

Potamogeton is an important food source for many waterfowl species and marsh birds. They consume the seeds or sometimes the entire plant (Martin 1951). Populations of some species of pondweeds can become so dense and abundant that weed control methods must be employed (Haynes 1978).

1. Leaf margins sharply serrate with small, conspicuous teeth and distinctly wavy or ruffled; leaves all submersed, sessile, often partially clasping stem; leaf tips rounded to slightly acute; stem flattened; fruit with a conical beak 2–3 mm long; turions present (hardened over-wintering buds produced later in season) ..... **3. Potamogeton crispus**
1. Leaf margins entire (rarely with tiny, unicellular denticles on young leaves), either ruffled, wavy, undulate, or flat; leaves submersed or floating, petiolate or sessile, but not clasping the stem; leaf tips obtuse, acute, or acuminate; stem rounded (terete); fruit with a beak usually < 1 mm long; turions rarely formed.

2. Submersed leaves narrowly linear or linear-lanceolate (< 3 mm wide), sessile, and usually 1–3 veined floating leaves, if present, < 10 cm long (measurement includes petiole and leaf blade); inflorescence (including peduncle and spike) < 6 cm long; fruit usually < 3 mm long; stipules of submersed leaves inconspicuous (< 2.5 cm long).

    3. Floating leaves often present, although sometimes lacking; stipular sheaths of submersed leaves fused (adnate) to base of leaf blades with free tips projecting as a ligule; fruit 3-keeled fruit wall paper thin and coiled embryo easily seen ..... **4. Potamogeton diversifolius**
    3. Floating leaves absent; leaf base axillary and free, not fused to stipules, forming a sheath or tube around stem above leaf; fruits 1-keeled or lacking a keel; fruit wall thick and embryo obscured.

        4. Fruit with a knobby, undulate, or dentate dorsal keel, peduncles (flower stalks) thickened towards apex (clavate) and short, usually < 3 cm long; inflorescences all axillary; nodes of stem lacking glands; stipules free (wrapped around stem, margins not fused) ..... **5. Potamogeton foliosus**
        4. Fruit lacking a keel, dorsally smooth and rounded; peduncles cylindrical, not thickened at apex and often longer, 1.5–8 cm long; inflorescences axillary or terminal; nodes of stem (at least some of them) with minute oil glands (wart-like & resinous); stipules free or with fused margins.

            5. Stipules with fused margins (connate), forming a tube surrounding the stem (extending a few millimeters up internode); leaf blades with 0–2 rows of lacunae (empty air cavities with thickened borders) on each side of midvein; inflorescence interrupted with 2–4 widely spaced whorls of flowers; fruit typically widest above middle with concave sides; beak of fruit occurring off to one side, not aligned in the middle ..... **9. Potamogeton pusillus**
            5. Stipules free (convolute), margins not fused (stipules form a sheath wrapping partially around stem); leaf blade with 1–5 rows of lacunae on each side of midvein; inflorescence with 1–3 crowded whorls of flowers; fruit widest at or below middle with rounded sides; beak of fruit centered in middle .....**2. Potamogeton berchtoldii**

2. Submersed leaves elliptic, ovate, lanceolate, or broadly linear-oblong (> 3 mm wide), sessile or petiolate, with 3 or more veins; floating leaves, if present, > 10 cm long (measurement includes petiole and leaf blade); inflorescence (including peduncle and spike) > 6 cm long; fruit usually > 3 mm long; stipules of submersed leaves conspicuous (> 2.5 cm long).

    6. Stems and petioles with raised blackish spots (wart-like dots); floating leaves cordate or truncate at base; margins of submersed leaves distinctly wavy or curly (bases rounded to truncate and petioles often with wedge-shaped wings) ..... **8. Potamogeton pulcher**
    6. Stems and petioles not spotted or with inconspicuous reddish-brown spots; floating leaves rounded, truncate or tapering at base; margins of submersed leaved broadly undulate or flat.

        7. Submersed leaves with petioles 4–13 cm long, usually much longer than blades; submersed leaf blades mostly flat to sometimes slightly wavy (1–3.5 cm wide); floating leaves usually present; fruit reddish, pinkish-brown to green, with a single, undulate dorsal keel with small knobs (lateral ridges rarely develop) .....**7. Potamogeton nodosus**

7. Submersed leaves sessile or with petioles 0.5–4 cm long, usually shorter than blade; submersed leaf blades either flat, undulate, folded, or curved (1–7.5 cm wide); floating or transitional leaves are occasionally present, but populations often consisting mostly submersed leaves; fruit with three low, rounded keels (one dorsal and two smaller lateral ridges).

   8. Submersed leaves either strongly folded longitudinally (convolute) and distinctly curved like a bow (arcuate) or strongly undulate and twisted; submersed leaf blades (median and upper) mostly broadly ovate, 2.5–7.5 cm wide with 23–49 veins (lowest leaves often lanceolate with fewer veins); fruits with a beak centered in the middle of fruit ..... **1. Potamogeton amplifolius**
   8. Submersed leaves often flat and straight or occasionally folded near the base and slightly curved or undulate; submersed leaf blades ovate, elliptic, oblong, lanceolate, or linear, 1.5–4.5 cm wide with 7–19 veins; fruits with a beak occurring near the edge of the fruit..... **6. Potamogeton illinoensis**

1. Potamogeton amplifolius Tuck. {large-leaved} — LARGE-LEAF PONDWEED; BROADLEAF PONDWEED; BIGLEAF PONDWEED; MUSKIE-WEED (Fig. 134).

Figure 134. *Potamogeton amplifolius*, Coldwater Spring Branch, Talladega Co., Alabama, 25 May 2018. Photos: Dan Spaulding.

Floating or submersed aquatic, perennial herb with rhizomes. Streams, creeks, rivers, springs, lakes, and ponds; flowers and fruits late May–September; uncommon in the Cumberland Plateau and Ridge & Valley; very rare in the Coastal Plain (Fig. 135). Native to Canada and the USA but more common in the northern half of North America and rare on the southeastern Coastal Plain (Kartesz 2018).

Potamogeton amplifolius has the largest leaves of any other species within the genus in Alabama (Haynes 2002). Large-Leaf Pondweed has both submersed and floating leaves (Fig. 136a), but some populations lack floating leaves or they are very scarce. Floating leaves are more leathery in texture and borne on long petioles (Fig. 136b). Submersed leaves are flaccid and sessile or have short petioles. Submersed leaves are often present in two forms. The blades can be folded along their mid-rib and curved like a bow (Fig. 136c) or wavy to twisted and only slightly folded (Fig. 134).

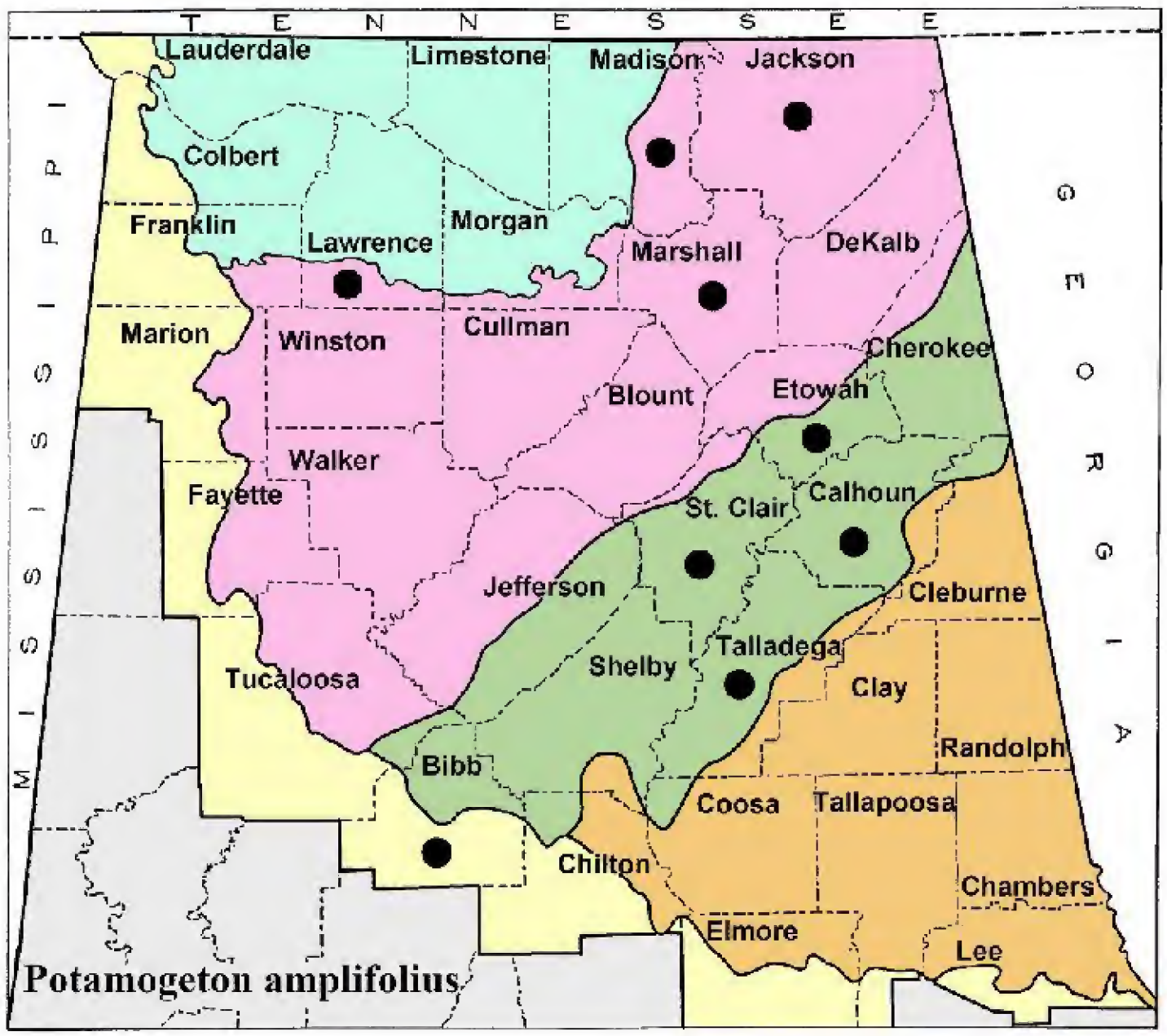


Figure 135. Distribution of *Potamogeton amplifolius* in northern Alabama.

(136a) Population in Cedar Creek. (136b) Floating leaves. (136c) Submersed leaves.

Figure 136. *Potamogeton amplifolius*, Talladega Co., Alabama, 4 Aug 2018. Photos: Dan Spaulding.

Potamogeton amplifolius is sometimes mistaken for *P. illinoensis*, which has narrower leaves with fewer veins. Both species have inflorescences with conspicuous spikes of flowers with thick peduncles (Fig. 137a) and their fruits have three, mostly smooth keels, one dorsal keel and two lateral (Fig. 137c). Large-Leaf Pondweed differs by having a beak located in the center the fruit (Fig. 137b), whereas Illinois Pondweed has a beak off to one side of the fruit.

(137a) Thick peduncle. (137b) Beak of fruit in center. (137c) Fruit with three rounded ridges.

Figure 137. *Potamogeton amplifolius,* Big Cove Creek, Etowah Co., Alabama, 11 Jul 2018. A. Fruiting spike. B. Close-up of fresh fruit. C. Dried fruit, AMAL, *Spaulding 15461*, Etowah Co., Alabama, 11 Jul 2018. Photos: Dan Spaulding.

2. Potamogeton berchtoldii Fieber subsp. **berchtoldii** {for Freidrich von Berchtold, 1781-1876, Austrian botanist} — SLENDER PONDWEED; BERCHTOLD'S PONDWEED (Fig. 138). [*Potamogeton pusillus* L. ssp. *tenuissimus* (Mert. & W.D.J. Koch) Haynes & C.B. Hellquist; *Potamogeton pusillus* var. *tenuissimus* Mert. & W.D.J. Koch]

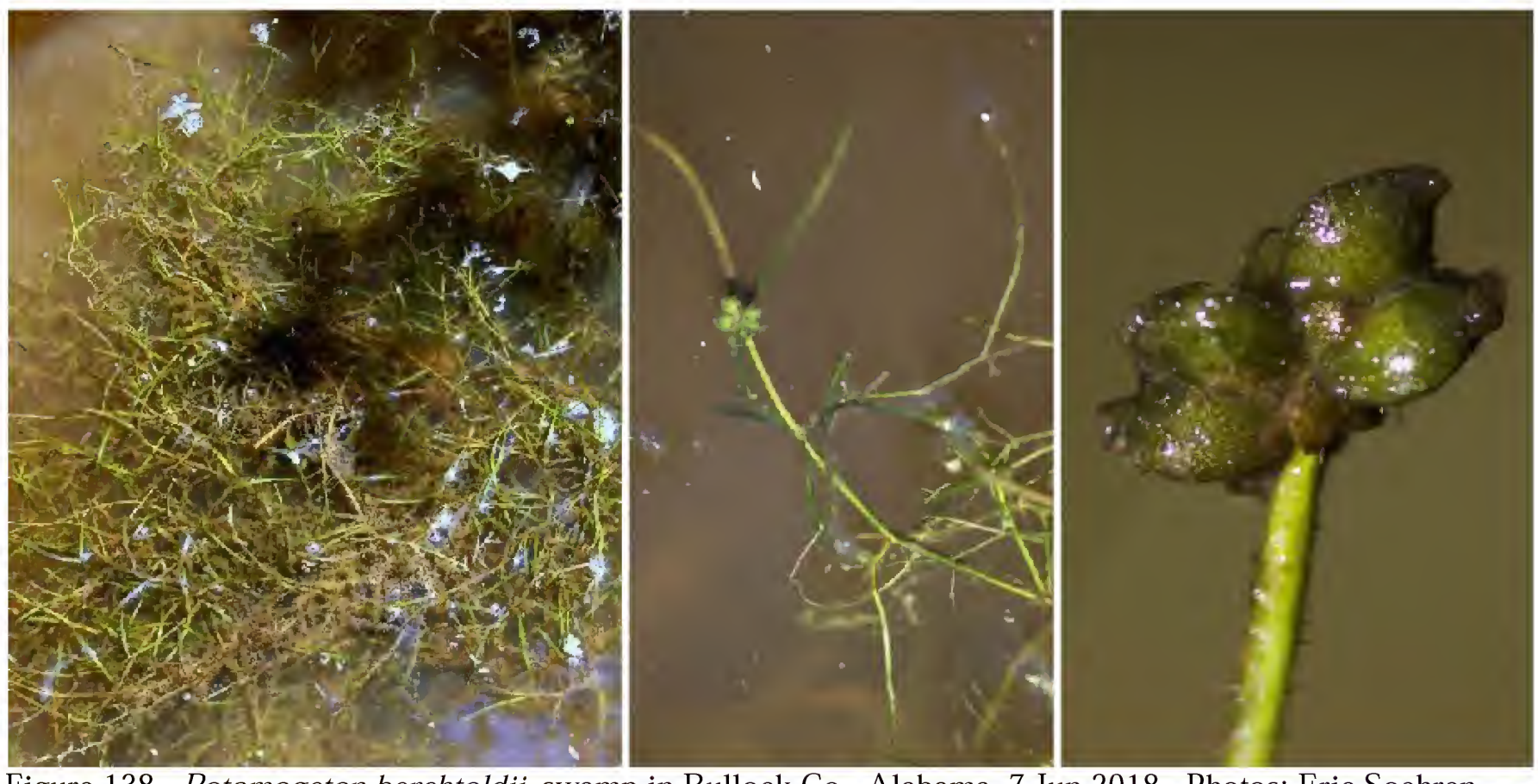


Figure 138. *Potamogeton berchtoldii*, swamp in Bullock Co., Alabama, 7 Jun 2018. Photos: Eric Soehren.

Submersed aquatic, perennial herb. Lakes, ponds, rivers, streams, swamps, and ditches; flowers and fruits May–September; uncommon in the Highland Rim; rare in the Cumberland Plateau (Tennessee River); frequent in the Coastal Plain (Fig. 139). Native to North America (Canada & USA), Europe, the Middle East, and Asia (Youhao et al. 2010).

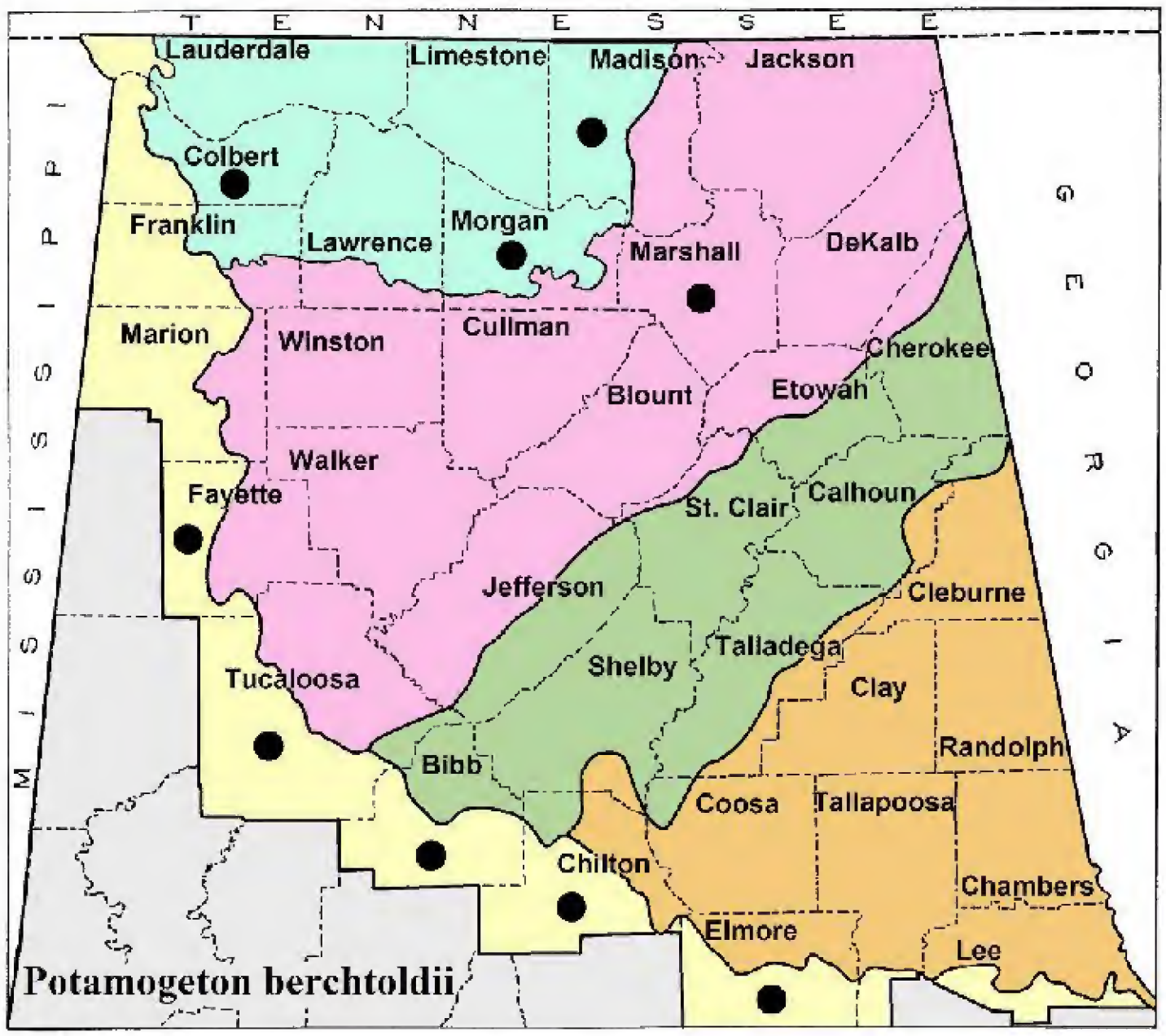


Figure 139. Distribution of *Potamogeton berchtoldii* in northern Alabama.

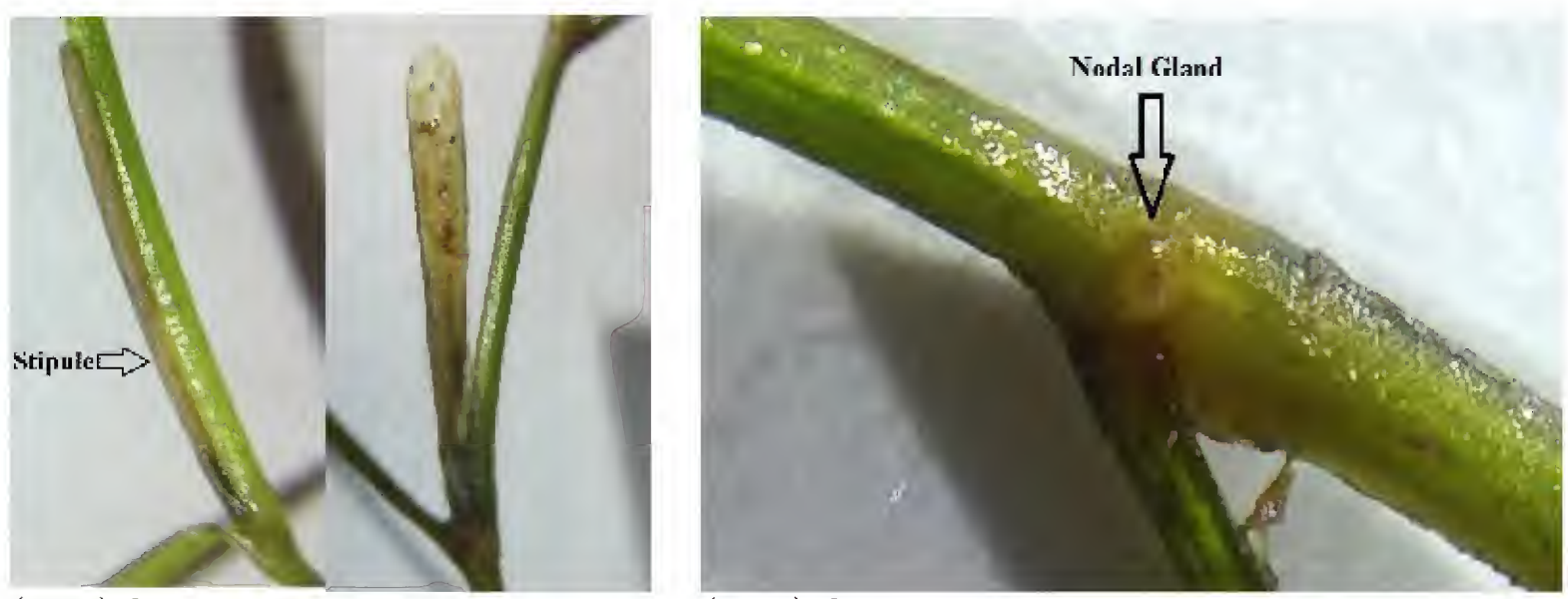
Potamogeton berchtoldii subsp. *berchtoldii* is easily identified by the following characters: inflorescence with crowded whorls of flowers (Fig. 140a); fruit rounded and widest at or below the middle with a beak located in the center (Fig. 140b); and linear leaves with 1–5 rows of lacunae (air spaces) on each side of the midvein (Fig. 140c). *Potamogeton berchtoldii* dies back at the end of the growing season, surviving winter by turions (over-wintering buds that detach and remain dormant underwater until spring).

Three closely related taxa are occasionally recognized as subspecies or species (Haynes & Hellquist 2000b; Les et al. 2009). *Potamogeton gemmiparus* (J.W. Robbins) J.W. Robbins ex Morong [*P. berchtoldii* subsp. *gemmiparus* (J.W. Robbins) Les & Tippery] has single-veined, subulate leaves and is confined to New England and adjacent Canada. *Potamogeton clystocarpus* Fern. [*P. berchtoldii* subsp. *clystocarpus* (Fern.) Les & Tippery] has keeled fruits and is known from only one county in Texas. *Potamogeton groenlandicus* Hagstr. [*P. berchtoldii* subsp. *groenlandicus* (Hagstr.) Feilberg] has leaves with 7–11 veins and is endemic to Greenland.

Haynes and Hellquist (2000b) treated *Potamogeton berchtoldii* subsp. *berchtoldii* and subsp. *gemmiparus* together as a subspecies of *P. pusillus* but recognized subsp. *clystocarpus* and subsp. *gemmiparus* as distinct species. *Potamogeton berchtoldii* differs from *P. pusillus* by having stipules that partially overlap the stem and easily separate from it (Fig. 141a). *Potamogeton pusillus* has stipules that are fused along their margins, forming a tube around the stem. *Potamogeton berchtoldii* and *P. pusillus*, unlike *P. foliosus*, have nodal glands that look like amber warts (Fig. 141b).

(140a) Flowers in tight clusters. (140b) Fruits crowded; beak centered in middle. (140c) Leaf with lacunae.

Figure 140. *Potamogeton berchtoldii*. A. Jefferson Co., Wisconsin, 15 Jun 2018. Photo: Brenton Butterfield. B–C. Swamp in Bullock Co., Alabama, 18 May 2018. Photos: Dan Spaulding.



(141a) Stipules free; margins not fused. (141b) Glands occur on both sides of most nodes.

Figure 141. *Potamogeton berchtoldii*, Bullock Co., Alabama, 18 May 2018. Photos: Dan Spaulding.

3. Potamogeton crispus L. {curly} — CURLY PONDWEED; CURLY MUCKWEED; CURLED PONDWEED; CRISP PONDWEED (Fig. 142).

Figure 142. *Potamogeton crispus*, Chagrin Lake, Cuyahoga Co., Ohio, 9 May 2019. Photos: Mark Warman.

Submersed aquatic, perennial herb with slender rhizomes. Lakes, ponds, rivers, creeks, streams, swamps, and brackish bays along the coast; flowers and fruits May–September; uncommon in the Highland Rim, Cumberland Plateau, and lower Coastal Plain (Mobile and Baldwin counties); rare in the Ridge & Valley (Fig. 143). Native to Europe, Asia, and Africa; introduced in the Pacific islands, New Zealand, and North America to South America (Youhao et al. 2010). The first report of *Potamogeton crispus* in North America occurred in the mid-19th Century, and the species quickly spread in the early 20th Century to most of the conterminous USA and southern Canada (Stuckey 1979). The first known collections for Alabama were made in 1943 (Bouldan et al. 1994).

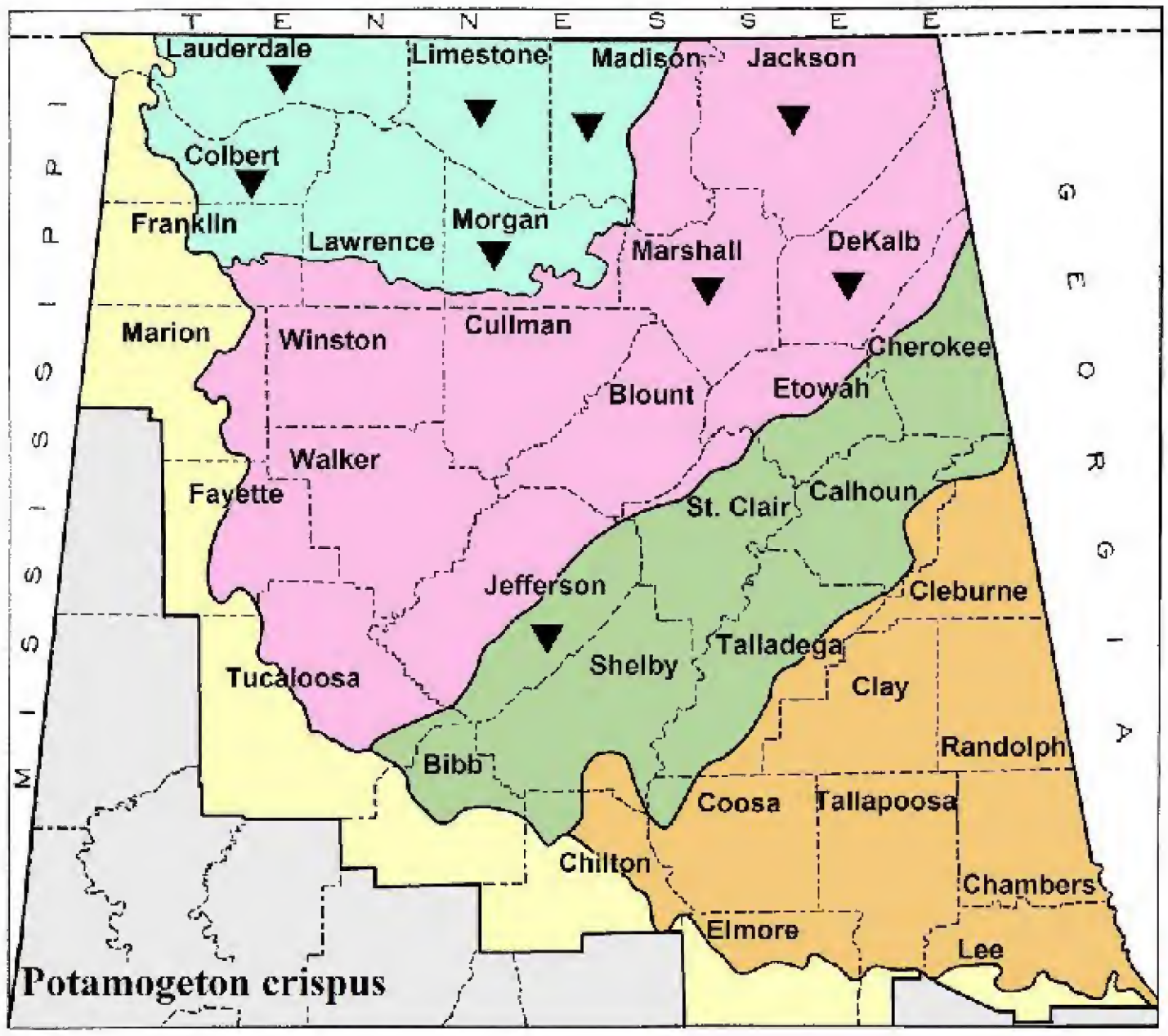


Figure 143. Distribution of *Potamogeton crispus* in northern Alabama.

Curly Pondweed is an aggressive exotic weed that invades clear, turbid, or polluted fresh to brackish waters. It has become a serious pest in some streams, rivers, and lakes utilized for recreation and navigation (Stuckey 1979). *Potamogeton crispus* grows in submerged colonies connected by rhizomes. It can be easily distinguished from other *Potamogeton* species by its flattened stems and oblong, sessile or clasping leaves with conspicuously serrate, wavy margins (Fig. 144). The flowers (Fig. 145a) produce a distinct fruit with a peculiar cone-shaped beak, 2–3 mm long (Fig. 145b).

Potamogeton crispus also spreads vegetatively by turions (Fig. 146a–c), which are formed by shortening of internodes of the stem apex (Haynes 1978). Following turion development, the parent plants will soon decay, leaving only the hardened modified shoots (turions) that remain dormant through winter and produce new cloned populations in spring (Haynes & Hellquist 2000b).

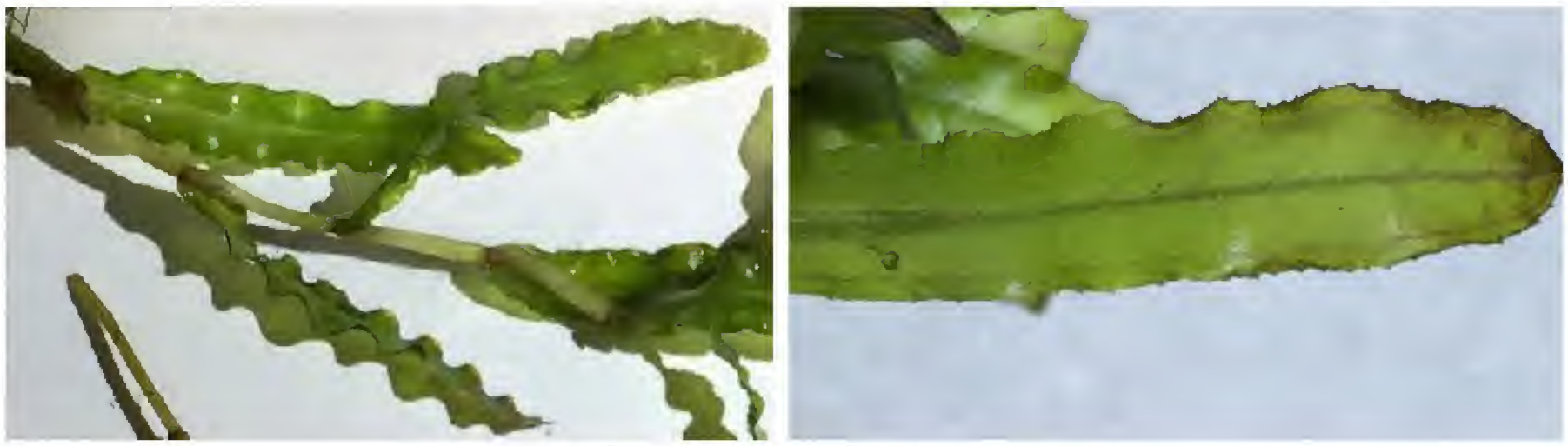


Figure 144. *Potamogeton crispus*, Valley Creek, Jefferson Co., Alabama, 30 Jul 2018. Leaves partially clasp a flattened stem and leaf margins are finely toothed and wavy (crisped). Photos: Dan Spaulding.

(145a) Inflorescence with mature flowers. (145b) Fruits with long, slender beaks.

Figure 145. *Potamogeton crispus.* A. South Slang Creek, Addison Co., Vermont, 29 Jun 2016. Photos: Susan Elliott. B. UNA, *Meigs, Wiersema, & Horn 203*, Shades Creek, Jefferson Co., Alabama, 9 May 1981. Photos: Dan Spaulding.

(146a) Turion forming. (146b) Turion at maturity. (146c) Turion producing new plant.

Figure 146. *Potamogeton crispus*. A. Valley Creek, Jefferson Co., Alabama, 30 Jul 2018. Photo: Dan Spaulding. B. Pond in Medina Co., Ohio, 25 Jul 2017. Photo: Mark Warman. C. Mogadore Reservoir, Portage Co., Ohio, 27 Jul 2017. Photo: Mark Warman.

4. Potamogeton diversifolius Raf. {diverse-leaved} — WATER-THREAD PONDWEED; COMMON SNAILSEED PONDWEED; DIVERSE-LEAF PONDWEED (Fig. 147). [*Potamogeton capillaceus* Poir.]

Figure 147. *Potamogeton diversifolius*, pond in Cleburne Co., Alabama, 20 May 2018. Photo: Dan Spaulding.

Floating or submersed aquatic, perennial herb with rhizomes. Ponds, lakes, swamps, marshes, ditches, mudflats, and shallow waters of rivers, creeks, and streams; flowers and fruits late April–October; frequent throughout Alabama (Fig. 148). Native to Mexico and almost the entire USA; probably the most common *Potamogeton* in the southeastern USA (Haynes & Hellquist 2000b).

Potamogeton diversifolius typically has some floating leaves with expanded blades, but its most diagnostic characters are its linear, submersed leaves, with stipules that are fused (adnate) to the leaf base with the free tip extending out as a ligule (Fig. 149). The adnate portion is less than 1/2 the length of the free ligule. This character makes the leaf blade appear to be attached near the upper portion of a sheath, partially clasping the stem. A terrestrial form with shortened internodes and mostly dilated leaves can occur in very shallow water or on exposed mudflats and shores (Fig. 150).

Inflorescences of *Potamogeton diversifolius* are dimorphic. The emersed flower spike is cylindric, 6–15 mm long (Fig. 151), and the submersed spike of flowers is produced in head-like clusters, 2–3 mm long (Fig. 152a). Fruits have three knobby keels (Fig. 152b) and a very thin fruit wall, clearly revealing the strongly coiled embryo (Fig. 152c), hence the name "snailseed" pondweed. This species fruits freely with or without floating leaves (Reznicek & Bobbette 1976).

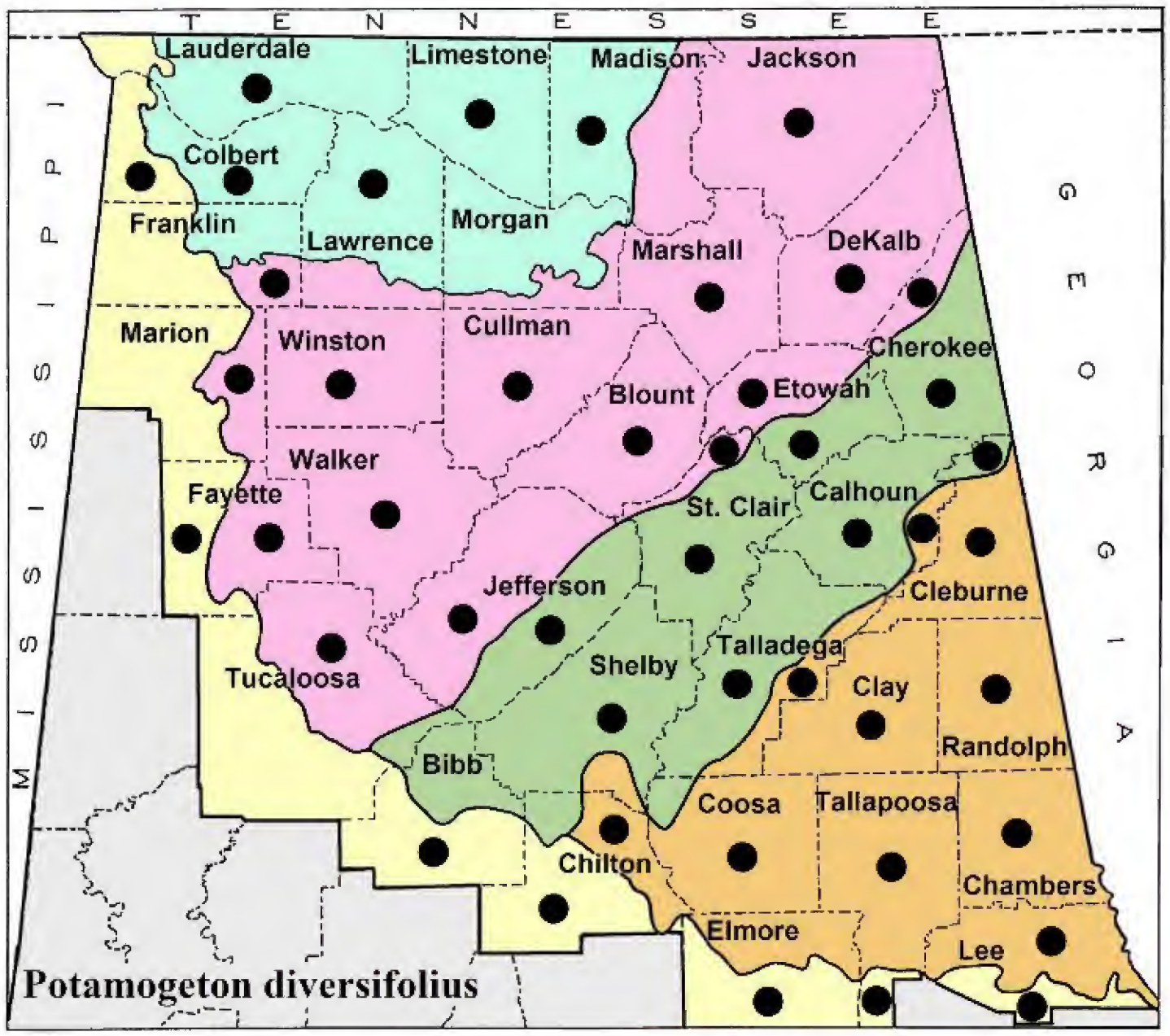
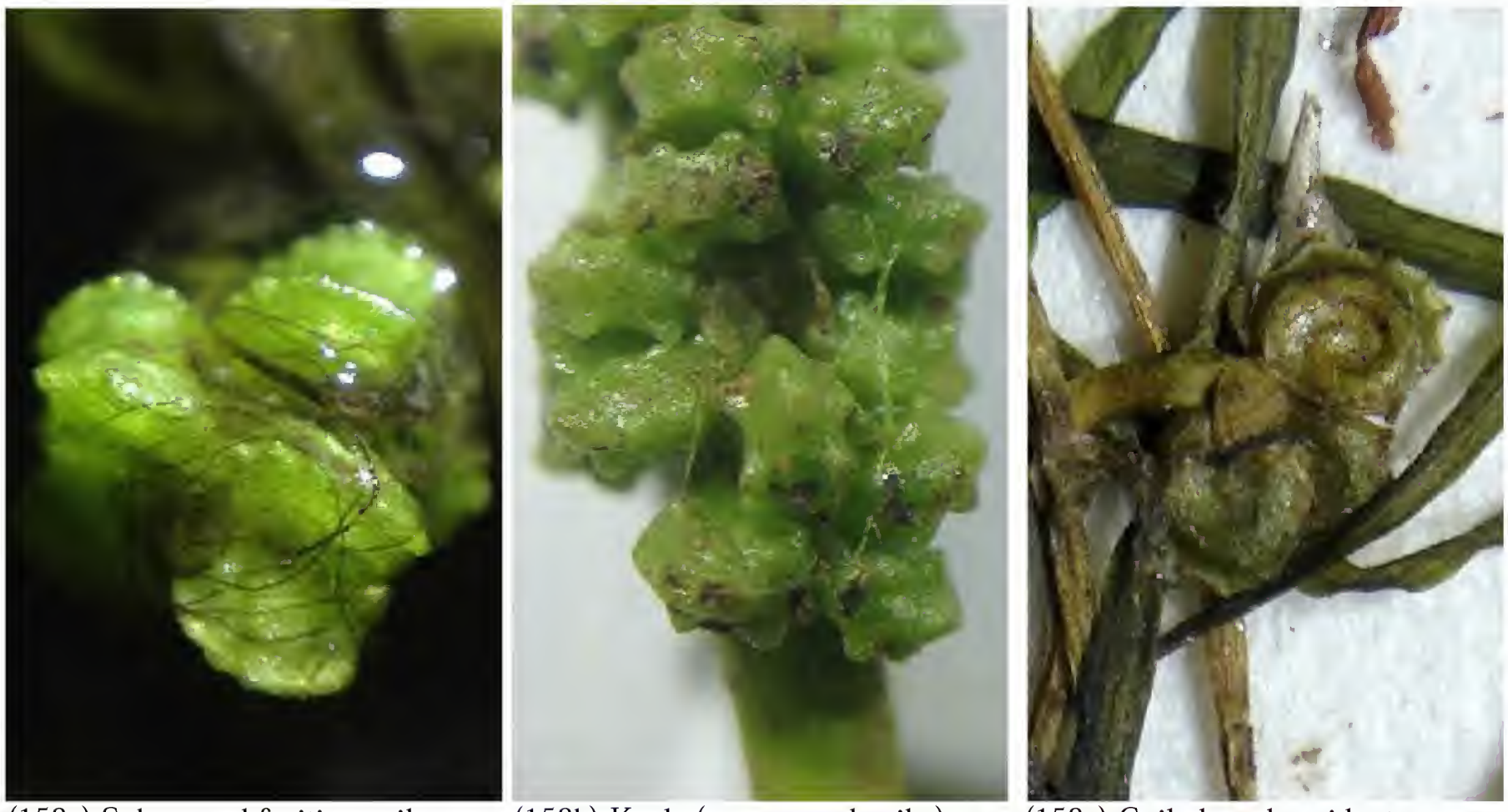


Figure 148. Distribution of *Potamogeton diversifolius* in northern Alabama.

Figure 149. *Potamogeton diversifolius*, floating leaves and submersed leaves with a close-up of adnation of stipule and leaf on submersed leaves. Plants from South Branch Cane Creek, Calhoun Co., Alabama, 24 May 2018. Photos: Dan Spaulding.

Figure 150. *Potamogeton diversifolius* population showing numerous leaves with expanded blades [growing with *Myriophyllum aquaticum*], Jefferson Co., Alabama, 2 Jun 2018. Photo: Dan Spaulding.

Figure 151. *Potamogeton diversifolius*, with emersed flowering spike, Ocean Co., New Jersey, 3 Aug 2017. Photos: Jason Ksepka.



(152a) Submersed fruiting spike. (152b) Keels (on emersed spike). (152c) Coiled seeds evident.

Figure 152. *Potamogeton diversifolius*. A. Cleburne Co., Alabama, 20 May 2018. B. Jefferson Co., Alabama, 2 Jun 2018. C. JSU, *Spaulding 10910*, Cleburne Co., Alabama, 8 Aug 2000. Photos: Dan Spaulding.

5. Potamogeton foliosus Raf. subsp. **foliosus** {leafy} — LEAFY PONDWEED (Fig. 153). [*Potamogeton curtissii* Morong; *Potamogeton foliosus* var. *macellus* Fern.]

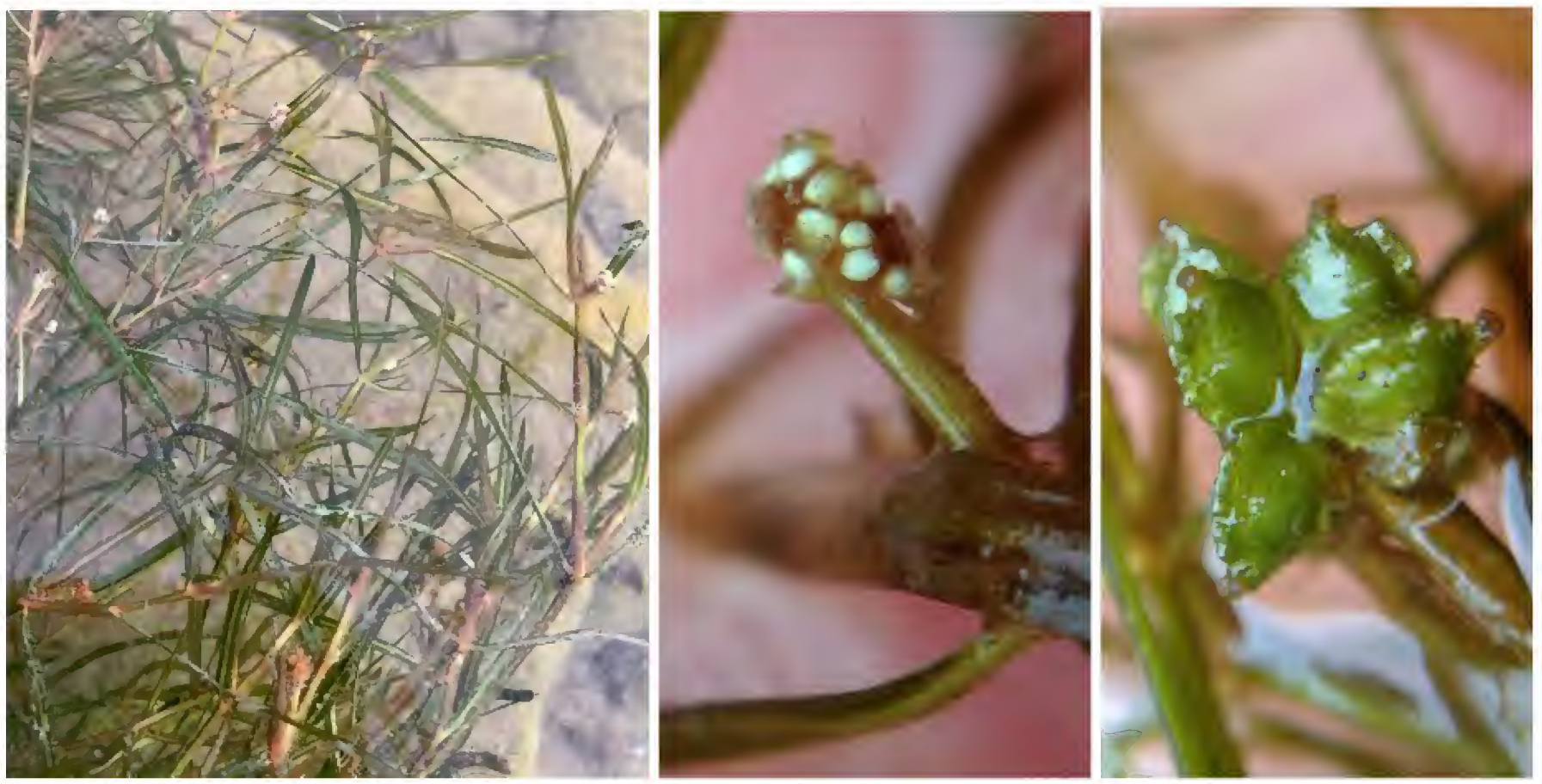


Figure 153. *Potamogeton foliosus*, small creek, Calhoun Co., Alabama, 21 May 2018. Photos: Dan Spaulding.

Submersed aquatic, perennial herb. Rivers, streams, creeks, lakes, ponds, and springs; flowers and fruits May–October; uncommon in the Highland Rim, Cumberland Plateau, and Ridge & Valley; rare in the Coastal Plain (Fig. 154). Native to almost all of North America south through Mexico to Costa Rica (Haynes & Hellquist 2000b).

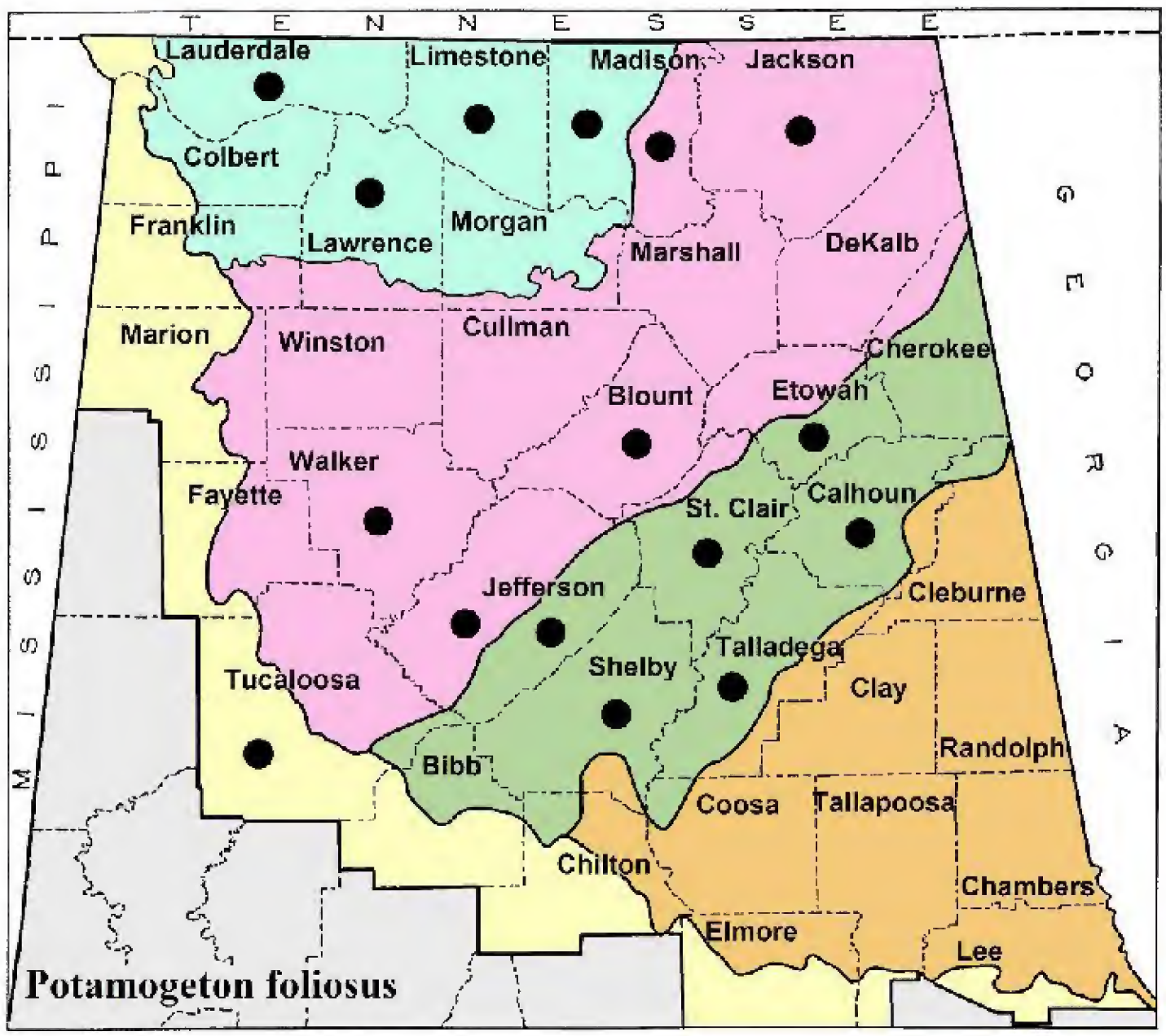


Figure 154. Distribution of *Potamogeton foliosus* in northern Alabama.

Because *Potamogeton pusillus* and *P. berchtoldii* have only submersed linear leaves, they are often confused with *P. foliosus*. However, *P. foliosus* stems lack nodal glands, its fruits are keeled on the back, and its stipules are fused (connate). *Potamogeton pusillus* and *P. berchtoldii* have stems with nodal oil glands, their fruits are rounded on back, and their stipules are free (convolute). *Potamogeton foliosus* rarely has bands of lacunae on each side of midrib (0–2 rows), whereas *P. berchtoldii* always has prominent lacunae (1–5 rows) and *P. pusillus* lacks them entirely.

Only *Potamogeton foliosus* subsp. *foliosus* is found in Alabama; the other subspecies, *P. foliosus* subsp. *fibrillosus* (Fern.) Haynes & C.B. Hellquist [Fibrous Pondweed], occurs in the northwestern USA. This subspecies can be distinguished by its stipular tissue between the veins that decomposes, leaving only strands of fibrous veins (Haynes & Hellquist 2000b).

6. Potamogeton illinoensis Morong {of Illinois} — ILLINOIS PONDWEED; SHINING PONDWEED (Fig. 155). [*Potamogeton angustifolius* Bercht. & C. Presl; *Potamogeton heterophyllus* Schreb.; *Potamogeton lucens* auct. non L.]

Floating or submersed aquatic, perennial herb with rhizomes. Found mostly in calcareous waters of rivers, streams, ponds, and lakes; flowers and fruits late May–September; rare in the Ridge & Valley and Coastal Plain (Fig. 156). Native to the Americas; scattered throughout Canada and the contiguous USA, south through Mexico to South America (Haynes & Hellquist 2000b).

Figure 155. *Potamogeton illinoensis*, Baldwin Co., Alabama, 4 Sep 2018. Photo: Howard Horne.

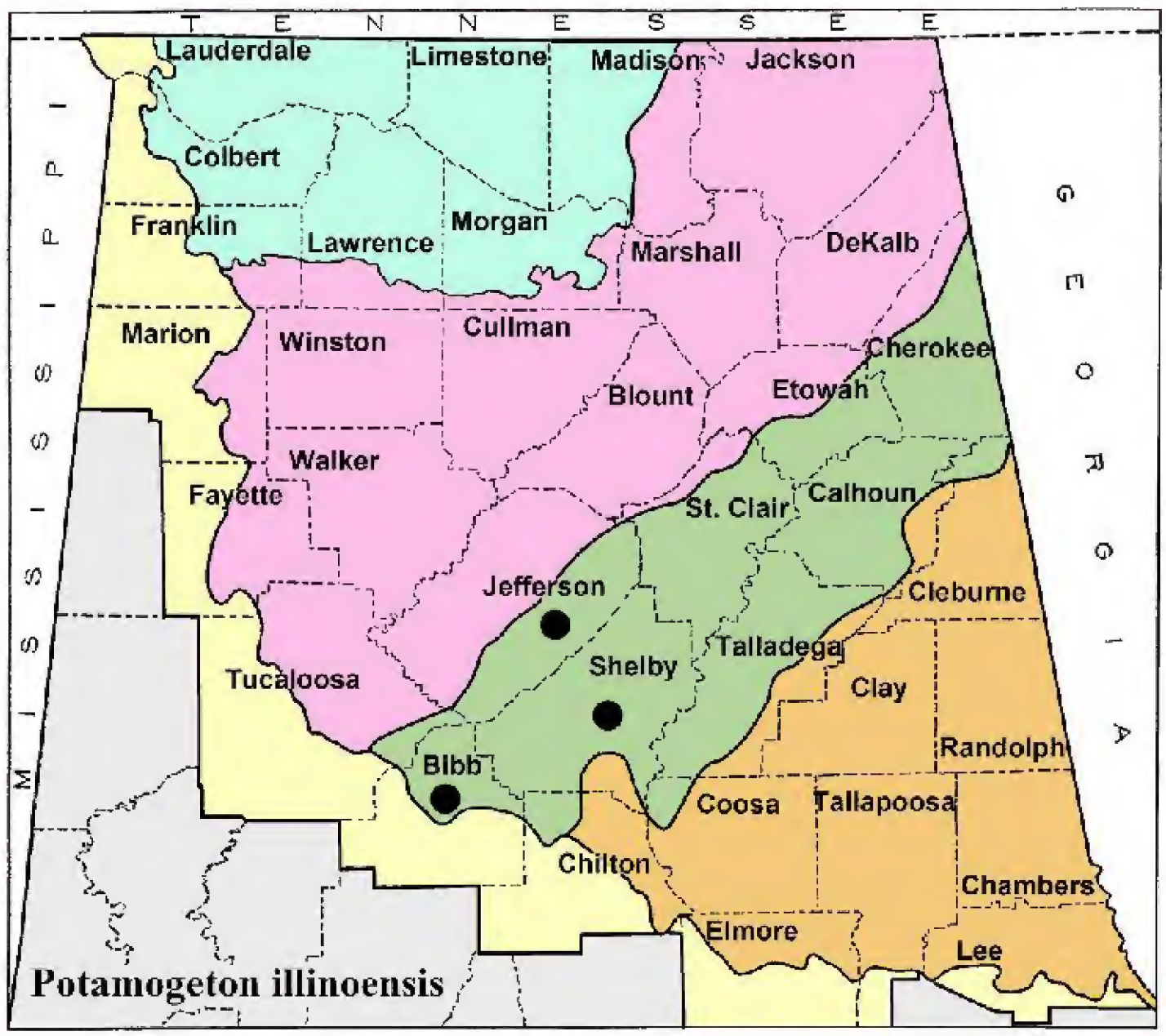


Figure 156. Distribution of *Potamogeton illinoensis* in northern Alabama.

Potamogeton illinoensis can be confused with *P. amplifolius* because both species have similar sized submersed leaves that are sessile or short-petioled. *Potamogeton illinoensis* differs by having fewer veins (< 20) and it submersed leaves (Fig. 157) are 3–4 times as long as broad and not completely folded or strongly curved (arcuate). The leaf apex of Illinois Pondweed is often abruptly acuminate, mucronate, or awl-shaped (Fig. 158). The fruit of *P. illinoensis* have a short beak (0.5 mm) that occurs near the edge rather than in the center. When floating leaves are present, *P. illinoensis* can be mistaken for *P. nodosus*, but the submersed leaves of *P. illinoensis* are either sessile or with petioles less than 4 cm long (Fig. 159a). *Potamogeton nodosus* submersed leaves have long petioles that are more than 4 cm long. The fruits of *P. illinoensis* (Fig. 159b–c) are greenish with three mostly smooth keels; *P. nodosus* fruits are typically reddish (when mature) with only a single, knobby dorsal keel.

Figure 157. *Potamogeton illinoensis*, Santa Clara Co., California, 17 Jul 2012. Photo: Edward Rooks.

Figure 158. *Potamogeton illinoensis* floating and submersed leaves, some with awl-shaped tips, in shallow water of Little Schultz Creek, Bibb Co., Alabama, 18 Jul 2018. Photos: Wayne Barger.

(159a) Submersed leaves short-petioled. (159b) Fruiting spike. (159c) Fruit 3-keeled (2 showing).

Figure 159. *Potamogeton illinoensis*. A. Little Schultz Creek, Bibb Co., Alabama, 18 Jul 2018. Photo: Wayne Barger. B–C. BRIT, *Kral & Moffett 90113*, Little Schultz Creek, Bibb Co., Alabama, 14 Aug 2000. Photo: Dan Spaulding.

7. Potamogeton nodosus Poir. {knotty} — LONGLEAF PONDWEED; AMERICAN PONDWEED; KNOTTY PONDWEED (Fig. 160). [*Potamogeton americanus* Cham. & Schlecht.; *Potamogeton fluitans* Roth; *Potamogeton lonchites* Tuck.]

Figure 160. *Potamogeton nodosus*, Franklin Co., Alabama, 22 Sep 2018. Photo: Dan Spaulding.

Floating or submersed aquatic, perennial herb with elongated rhizomes. Lakes, ponds, rivers, and streams; flowers and fruits May–September; frequent in the Highland Rim; uncommon in the Cumberland Plateau, Piedmont, and Coastal Plain; rare in the Ridge & Valley (Fig. 161). Native to the Americas; scattered throughout Canada and the contiguous USA, south through Mexico to South America (Haynes & Hellquist 2000b).

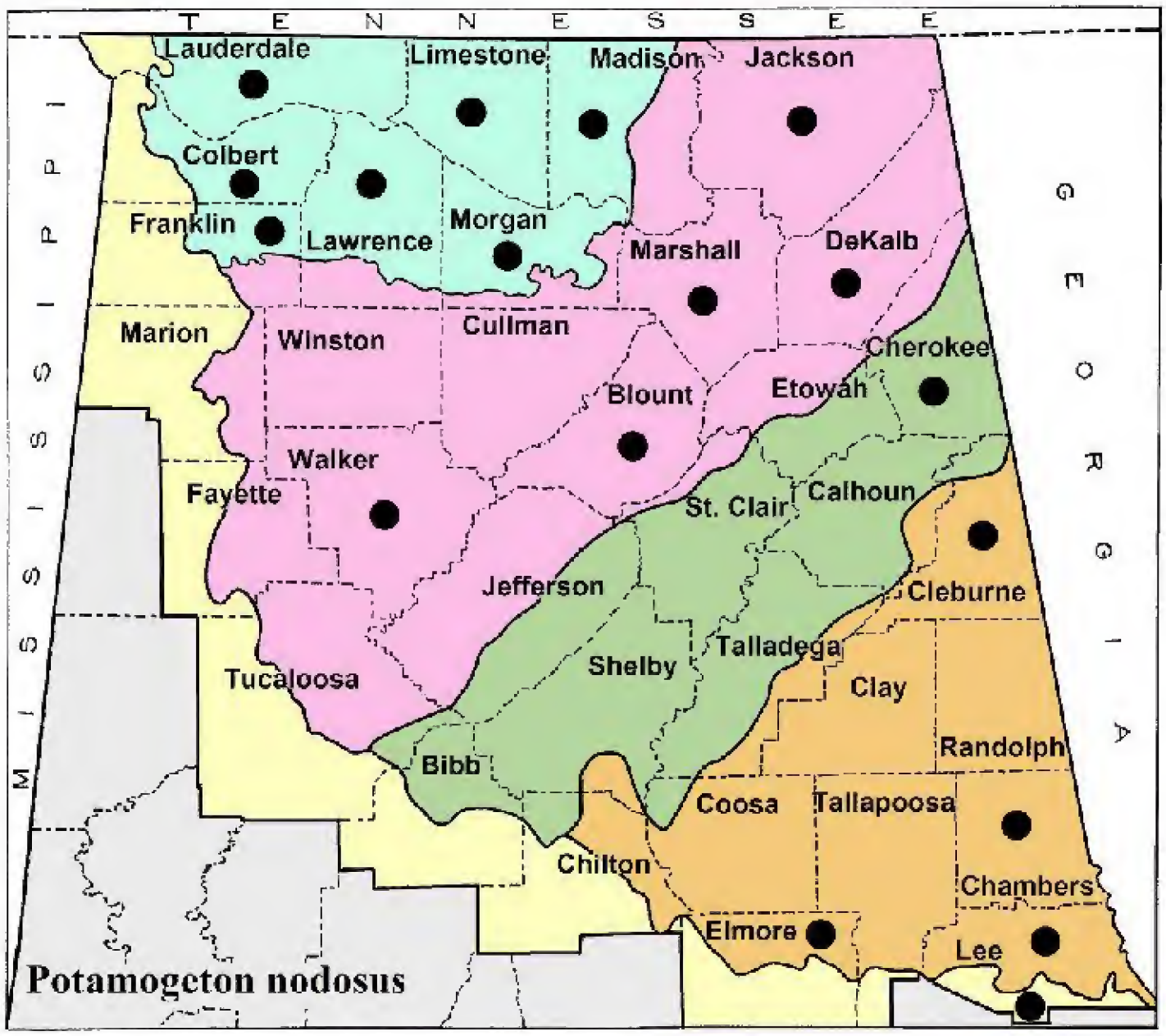
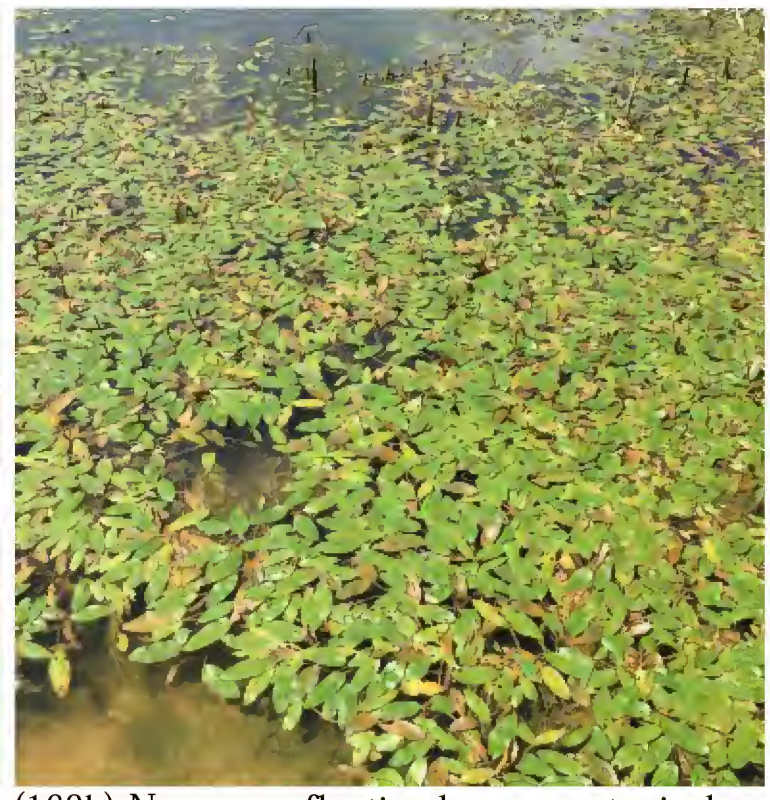


Figure 161. Distribution of *Potamogeton nodosus* in northern Alabama.

Figure 162. *Potamogeton nodosus*, Limestone Co., Alabama, 15 Jul 2018. Photo: Dan Spaulding.

Longleaf Pondweed often has numerous long-petioled, floating leaves with blades that are typically elliptic-oblong to lanceolate-oblong (Fig. 162). Its flowers are predominantly wind-pollinated (Philbrick & Anderson 1987) and the inflorescence is an elongated, compact spike held above the water on thick peduncles (Fig. 163a). This species often spreads by rhizome growth and can become locally abundant (Fig. 163b), covering large areas of the water surface (Haynes 1988).

(163a) Inflorescence with a thick peduncle.



(163b) Numerous floating leaves are typical.

Figure 163. *Potamogeton nodosus.* A. Tallapoosa River, Cleburne Co., Alabama, 14 Jul 2018. B. Pond in DeKalb Co., Alabama, 11 Aug 2018. Photos: Dan Spaulding.

Potamogeton nodosus is sometimes mistaken for *P. illinoensis*, but *P. nodosus* has submersed leaves with petioles > 4 cm long (Fig. 164a), and its fruits are often tan to reddish (Fig. 164b) with one undulate keel (Fig. 164c). In contrast, *P. illinoensis* has submersed leaves that are sessile or on short petioles (< 4 cm) and its fruits are greenish with three, mostly smooth keels.

(164a) Submersed leaves.

(164b) Fruiting spike.

(164c) Fruit with undulate keel.

Figure 164. *Potamogeton nodosus*. A. Cleburne Co., Alabama, 20 May 2018. B. DeKalb Co., Alabama, 11 Aug 2018. B. AMAL, *Spaulding 15546*, DeKalb Co., Alabama, 11 Aug 2018. Photos: Dan Spaulding.

Ribbon-Leaf Pondweed, *Potamogeton epihydrus* Raf. (Fig. 165a–b), superficially resembles *P. nodosus*, but *P. epihydrus* can be distinguished by its flattened stems and linear submersed leaf blades (< 6 mm wide) with prominent lacunar bands on each side of the midrib (Haynes 1980). *Potamogeton epihydrus* has been documented from the Coastal Plain of Lee County, as well as from 3 other counties south of the study area (Keener et al. 2019). It also occurs in adjacent Tennessee (Kartesz 2018) and is common in the northern USA and southern Canada (Haynes & Hellquist 2000b).

(165a) Floating leaves mostly oblong and submersed leaves linear.

(161b) Broad lacunar bands.

Figure 165. *Potamogeton epihydrus*. A. Thunder Bay, Ontario, Canada, 15 Aug 2017. Photo: Rob Foster. B. Submersed leaves, Wisconsin River, Lincoln Co., Wisconsin, 6 Jun 2017. Photo: Brenton Butterfield.

8. Potamogeton pulcher Tuck. {handsome} — SPOTTED PONDWEED; HEARTLEAF PONDWEED (Fig. 166).

Figure 166. *Potamogeton pulcher*, Butler Co., Alabama, 14 Apr 2010. Photo: Alvin Diamond.

Floating or submersed aquatic, perennial herb with rhizomes. Ponds, lakes, swamps, and slow moving to stagnant streams; flowers and fruits May–September; rare in the Highland Rim, Cumberland Plateau, Ridge & Valley, and Piedmont, frequent in the Coastal Plain (Fig. 167). Native to eastern North America from southern Canada south to east Texas and northern Florida (Haynes & Hellquist 2000b).

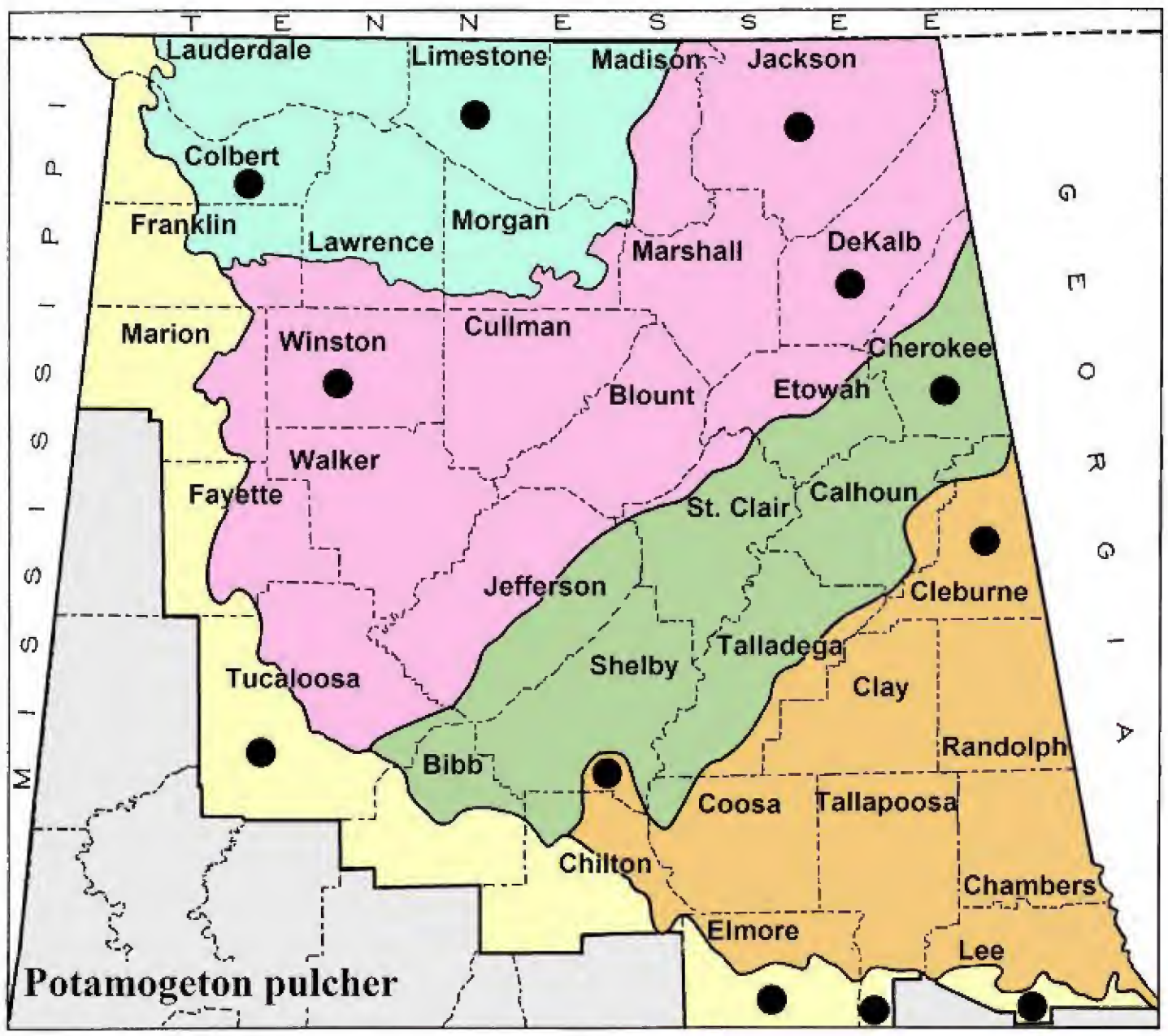


Figure 167. Distribution of *Potamogeton pulcher* in northern Alabama.

Potamogeton pulcher is a distinct pondweed that can be easily identified by its numerous floating leaves with cordate or truncate leaf bases (Fig. 168a–b), dark-spotted stems, and submersed lanceolate leaves with wavy margins and short, wedge-shaped petioles (Fig. 169).

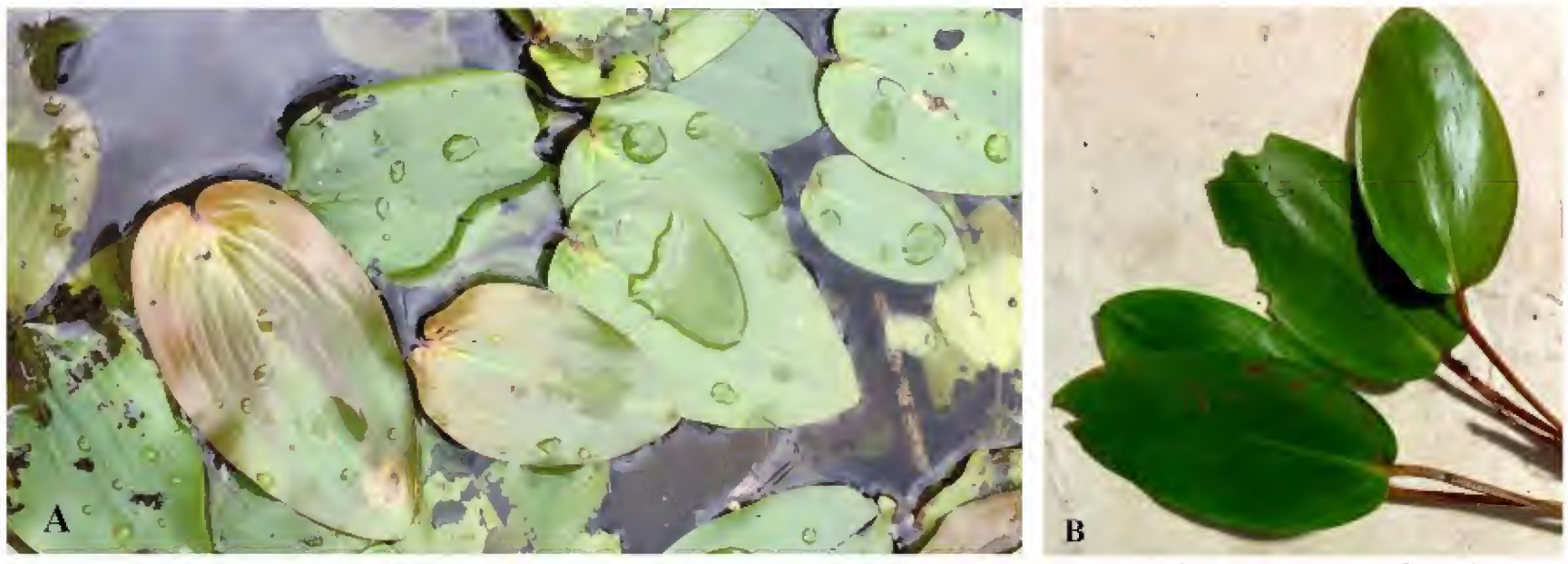


Figure 168. *Potamogeton pulcher*, floating leaves with cordate or truncate bases. A. Tallapoosa Co., Alabama, 28 May 2018. Photo: Dan Spaulding. B. Cleburne Co., Alabama, 11 Jun 2019. Photo: Melanie T. Spaulding.

Figure 169. *Potamogeton pulcher*, Tallapoosa Co., Alabama, 28 May 2018. Photos: Dan Spaulding.

Potamogeton amplifolius is similar in morphology to *P. pulcher*, but *P. amplifolius* differs by having floating leaves with mostly rounded bases, submersed leaves that are ovate with more than 20 veins, and stems lacking black spots (plants will occasionally have small, red-brown spots).

9. Potamogeton pusillus L. {very small} — SMALL PONDWEED (Fig. 170).

Figure 170. *Potamogeton pusillus*, spring in Etowah Co., Alabama, 11 July 2018. Photos: Dan Spaulding.

Submersed aquatic, perennial herb. Streams, rivers, lakes, and ponds; flowers and fruits May–September; uncommon throughout Alabama (Fig. 171). Widely distributed globally in the Northern Hemisphere; native to North America, South America, Eurasia, and Africa (Haynes & Hellquist 2000b).

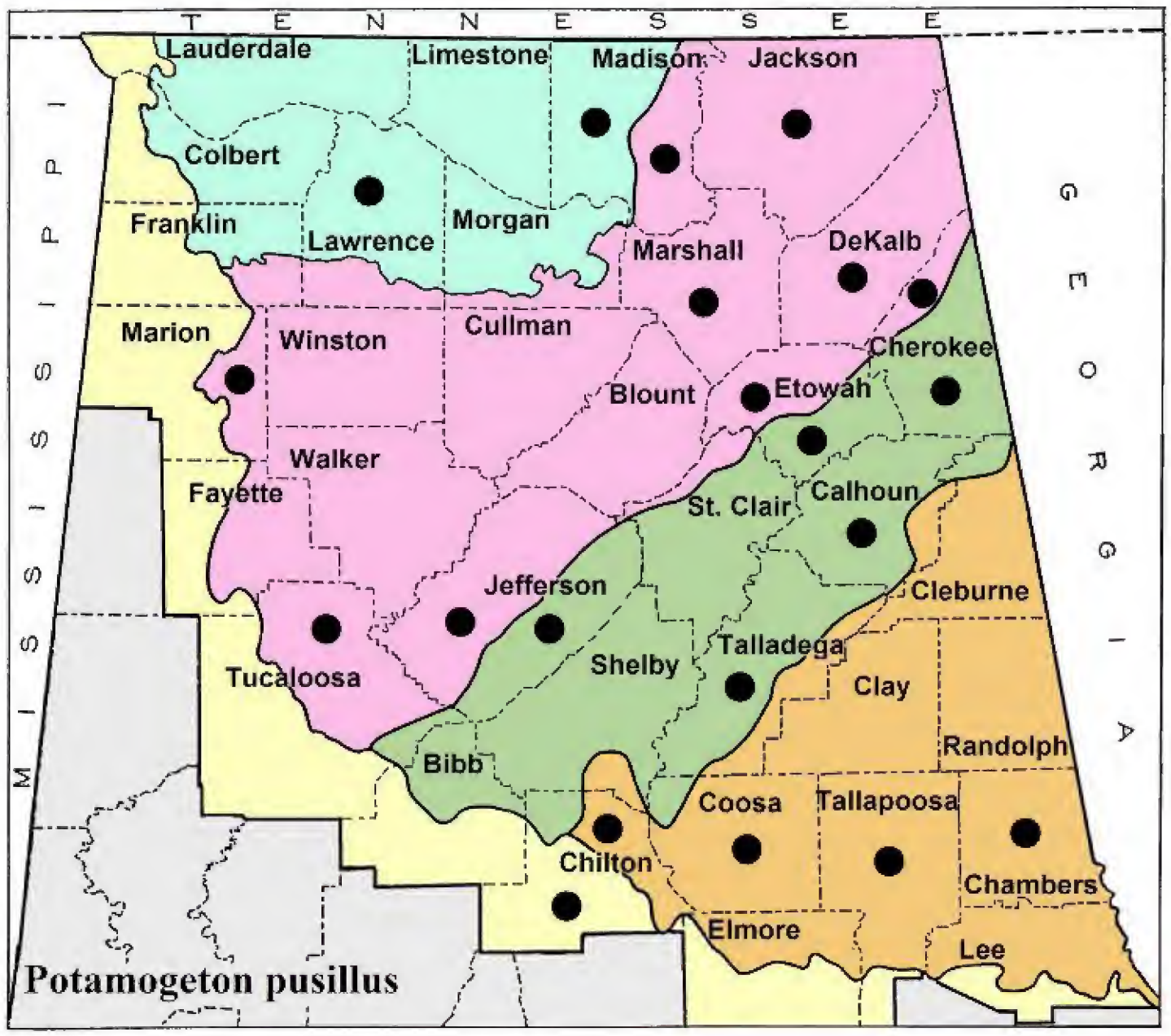


Figure 171. Distribution of *Potamogeton pusillus* in northern Alabama.

Potamogeton pusillus is very similar to *P. berchtoldii* and *P. foliosus*. Haynes (1974) treated *P. berchtoldii* as a variety of *P. pusillus*. The defining characters of *P. pusillus* are: its stipule margins being fused, forming a tube around stem (Fig. 172); most nodes having a pair of oil glands (Fig. 173a); leaves with 0–2 rows of lacunae (Fig. 173b); mature inflorescence with interrupted whorls of flowers/fruits (Fig. 174a–b); and fruits with concave sides and off-centered beaks (Fig. 174c). *Potamogeton berchtoldii* flowers are crowded, its fruits have rounded sides with beaks centered in the middle, the leaves have 1–5 rows of lacunae along the midrib, and its stipule margins are not fused. *Potamogeton foliosus* lacks nodal glands and its fruits have knobby keels.

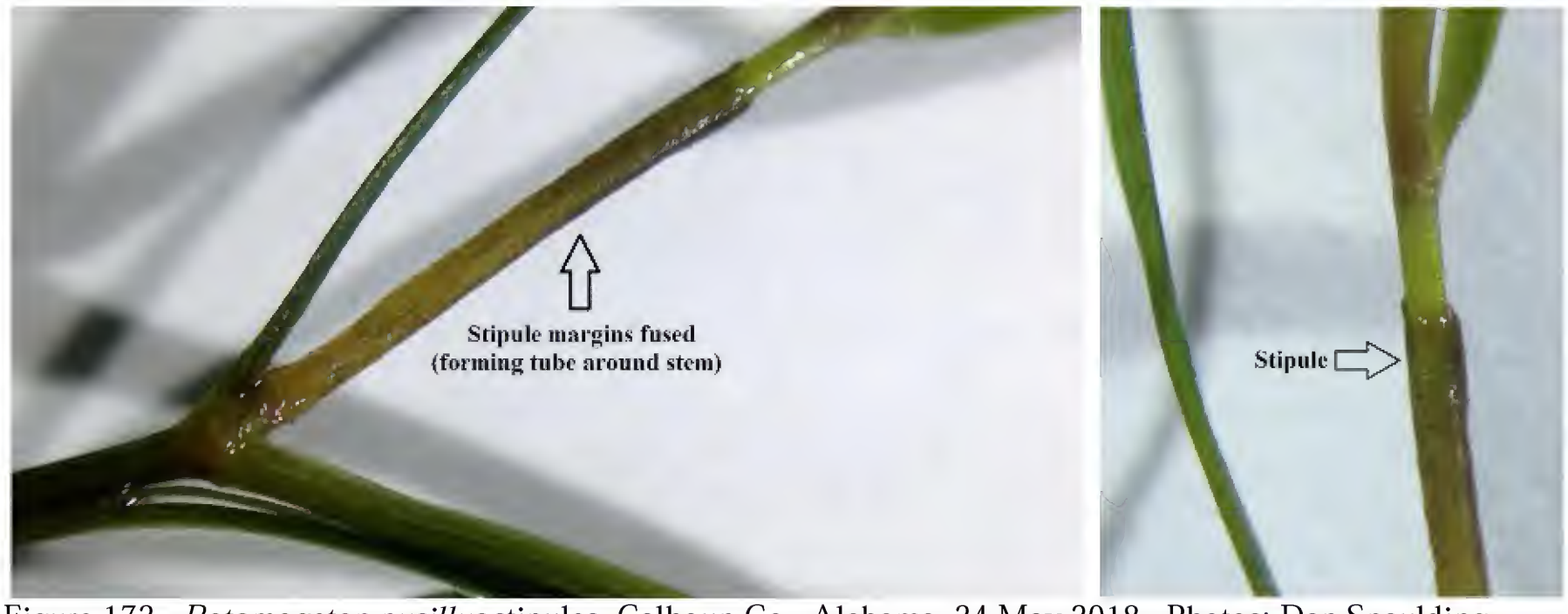


Figure 172. *Potamogeton pusillus* stipules, Calhoun Co., Alabama, 24 May 2018. Photos: Dan Spaulding.

(173a) Nodal oil gland.

(173b) Leaves usually lacking lacunae (banded air-spaces).

Figure 173. *Potamogeton pusillus*. A. Close-up of an oil gland at node, Calhoun Co., Alabama, 24 May 2018. B. Close-up of leaf, Etowah Co., Alabama, 11 Jul 2018. Photos: Dan Spaulding.

(174a) Spike of flowers.

(174b) Spike of fruits.

(174c) Beak off-center; sides concave.

Figure 174. *Potamogeton pusillus*. A–C. Etowah Co., Alabama, 11 Jul 2018. Photos: Dan Spaulding.

2. STUCKENIA C. Börner 1912

[Named after Wilhelm Adolf Stucken, 1860–1901, amateur German botanist and entomologist]

1. Stuckenia pectinata (L.) Börner {comb-like} — SAGO PONDWEED; FENNEL-LEAF PONDWEED; SAGO FALSE PONDWEED; FENNEL PONDWEED (Fig. 175). [*Coleogeton pectinatus* (L.) D.H. Les & Haynes; *Potamogeton pectinatus* L.]

Figure 175. *Stuckenia pectinata*, Prestile Stream, Aroostook Co., Maine, 29 Jul 2005. Photos: Don Cameron.

Submersed aquatic, perennial herb with rhizomes and tubers. Rivers, lakes, and bays along the coast; flowers and fruits June–September; very rare in the Highland Rim (Tennessee Valley district), and Cumberland Plateau (Sequatchie Valley district); rare in lower Coastal Plain (Fig. 176). In fresh or brackish waters on all continents in the Northern Hemisphere (Kaplan 2008).

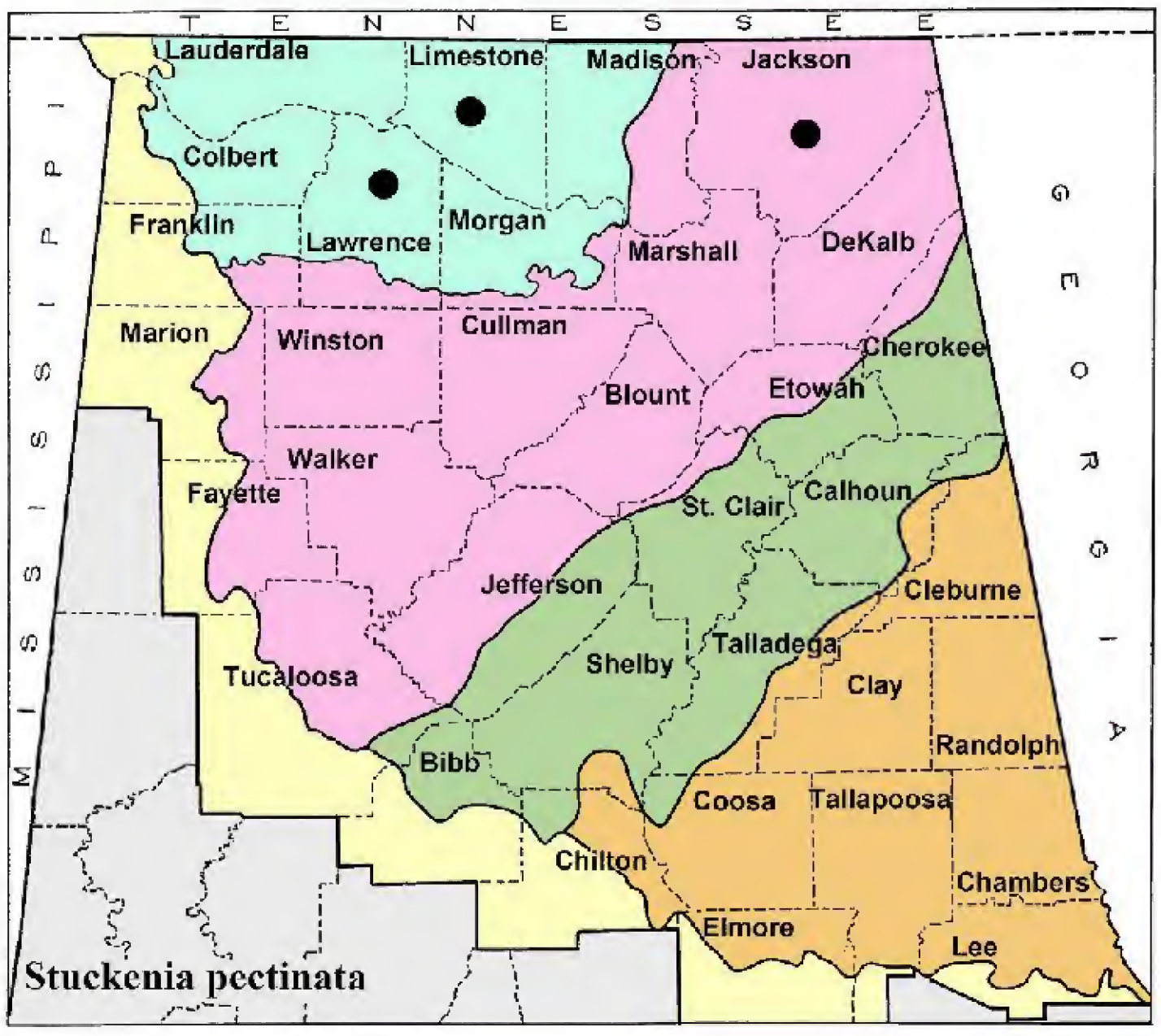


Figure 176. Distribution of *Stuckenia pectinata* in northern Alabama.

According to Haynes & Hellquist (2000b), the best diagnostic character differentiating *Stuckenia* from *Potamogeton* is the stipules. *Stuckenia* stipules are fused (adnate) with the basal portion of the leaf for at least 2/3 of the length, forming a long stipular sheath with a ligule (Fig. 177). *Stuckenia pectinata* has sessile, tubular leaves with air channels (lacunae) along the midribs (Fig. 178). Its inflorescences are on long, flexuous peduncles that float rather than being held above water (Holub 1997). The flowering spike has 2–5 whorls of flowers that are clustered together when immature but separate during anthesis (Fig. 179). Fruiting spikes are interrupted, and the fruits are greenish-brown to light brown with a beak off to one side (Fig. 180).

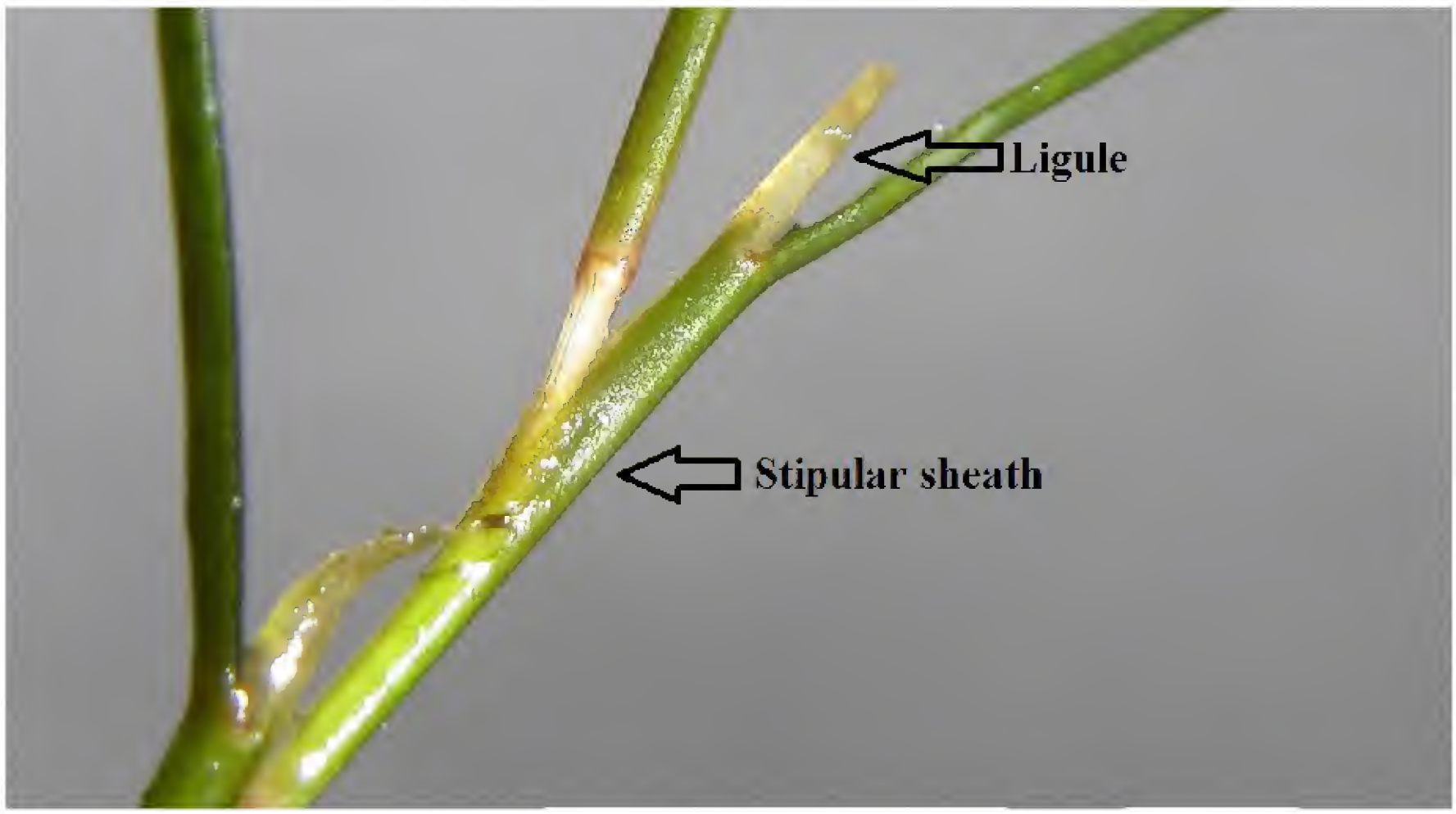


Figure 177. *Stuckenia pectinata* stipule, Mjindi, South Africa, 10 Nov 2017. Photo: Ricky Taylor.

Figure 178. *Stuckenia pectinata* leaves, Baldwin Co., Alabama, 4 Aug 2009. Photo: Howard Horne.

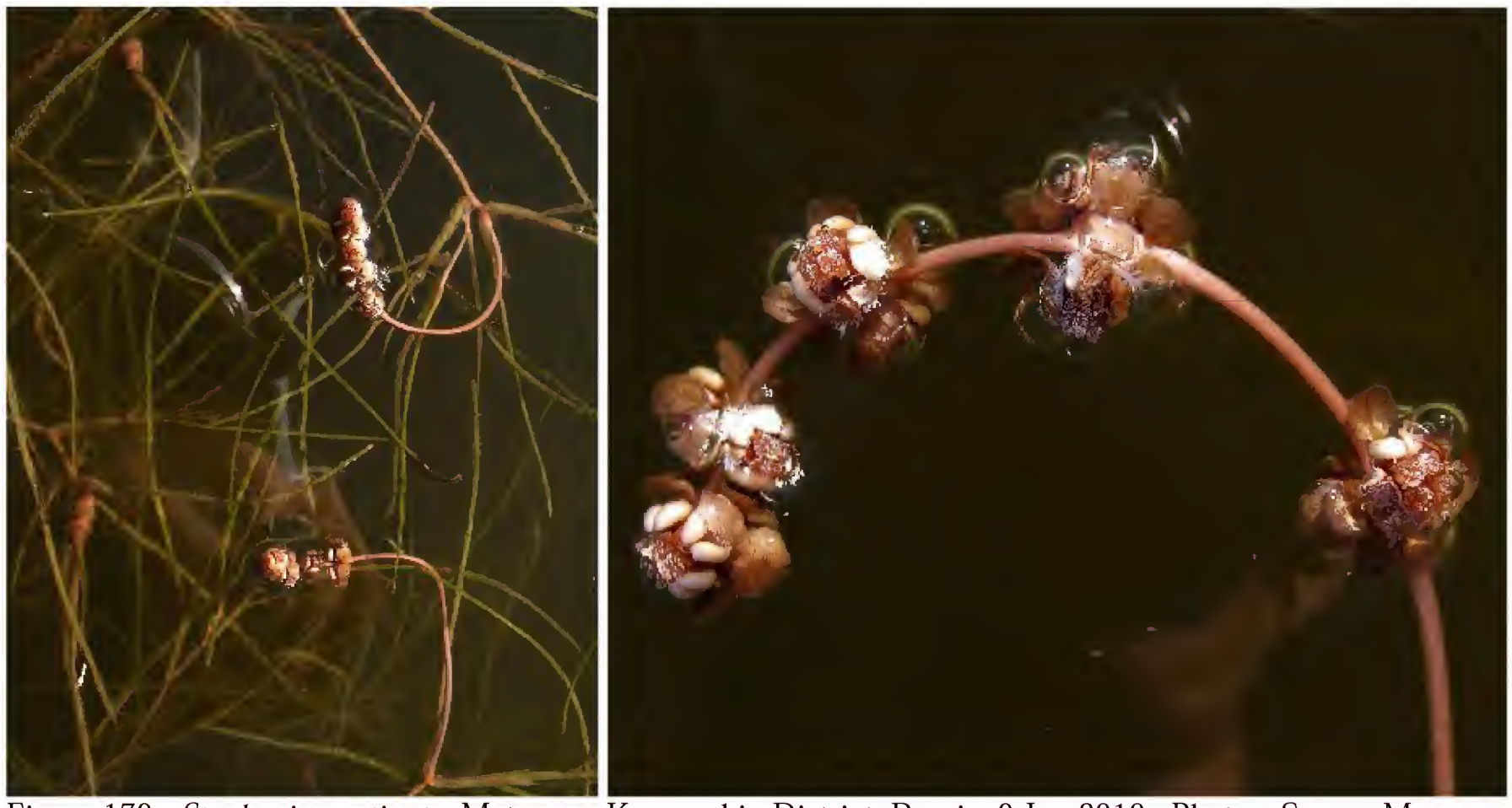


Figure 179. *Stuckenia pectinata*, Matveevo-Kurganskiy District, Russia, 9 Jun 2010. Photos: Sergey Mayorov.

Figure 180. *Stuckenia pectinata*. Orange Co., California, 28 Jun 2018. Photos: Ron Vanderhoff.

Sago Pondweed is rare in Alabama, known only from portions of the Tennessee River and in brackish waters of Mobile Bay. However, the widespread distribution of *Stuckenia pectinata* makes this pondweed a very valuable food source for waterfowl, marshbirds, and shorebirds. These birds readily consume the leaves, stems, rhizomes, and large seeds (Martin 1951). *Stuckenia* also reproduces vegetatively by underground tubers, which are eaten and spread by a variety of ducks, especially Canvasbacks (Haynes & Hellquist 2000b).

3. ZANNICHELLIA Linnaeus 1753

[Named in honor of Gian Girolamo Zannichelli, 1662-1729, a Venetian botanist]

1. Zannichellia palustris L. {of marshes} — HORNED PONDWEED; COMMON POOLMAT (Fig. 181). [*Zannichellia palustris* var. *major* (Hartm.) W.D.J. Koch]

Figure 181. *Zannichellia palustris*, Summit Co., Ohio, 28 Jul 2018. Photos: Mark Warman.

Submersed aquatic, annual herb. Lakes, rivers, springs, brackish bays and estuaries on the coast; flowers and fruits February–October; rare in the Highland Rim, Cumberland Plateau, and lower Coastal Plain (Fig. 182). Occurring nearly worldwide; found throughout North America, Mexico, Central America, South America, Eurasia, Africa, and Australia (Haynes & Hellquist 2000c).

Zannichellia palustris has long, linear leaves, mostly opposite or in pseudo-whorls and often rooting at the nodes (Fig. 183). It grows clonally in inland freshwater lakes or in shallow, brackish, coastal waters (Haynes & Holm-Nielsen 2001). In northern Alabama, this species has been collected sporadically in springs, reservoirs, and cooling channels at power plants, especially along the Tennessee River. The species is fairly frequent on the Coastal Plain in estuaries and bays of Mobile and Baldwin counties.

Horned Pondweed is an annual that does not reproduce vegetatively by leaf fragmentation, budding or turion formation; therefore, it requires seed production for survival (Haynes 1988). *Zannichellia* is monoecious and produces two unisexual flowers lacking a perianth, produced on sessile inflorescences within the leaf axil. Male flowers have a single stamen and female flowers have 4–5 separate carpels, enclosed by a membranous envelope (Haynes & Hellquist 2000c).

Pollen transfer takes place underwater, with most seeds developing from self-pollination; rarely are plants cross-pollinated (Guo et al. 1990). The pollination system of *Zannichellia* is unusual in that the stamen arches over the pistillate flower, releasing a gelatinous mass onto funnel-shaped stigmas, enabling reproduction (Haynes & Holm-Nielsen 2001). Fertilized carpels produce an axillary cluster of falcate or banana-shaped fruits (Fig. 184a), which is an achene on a short stalk with an undulate, dorsal keel and a conspicuous, horn-like beak (Fig. 184b). Various duck species are reported to consume the fruits and vegetative parts (Martin et al. 1951).

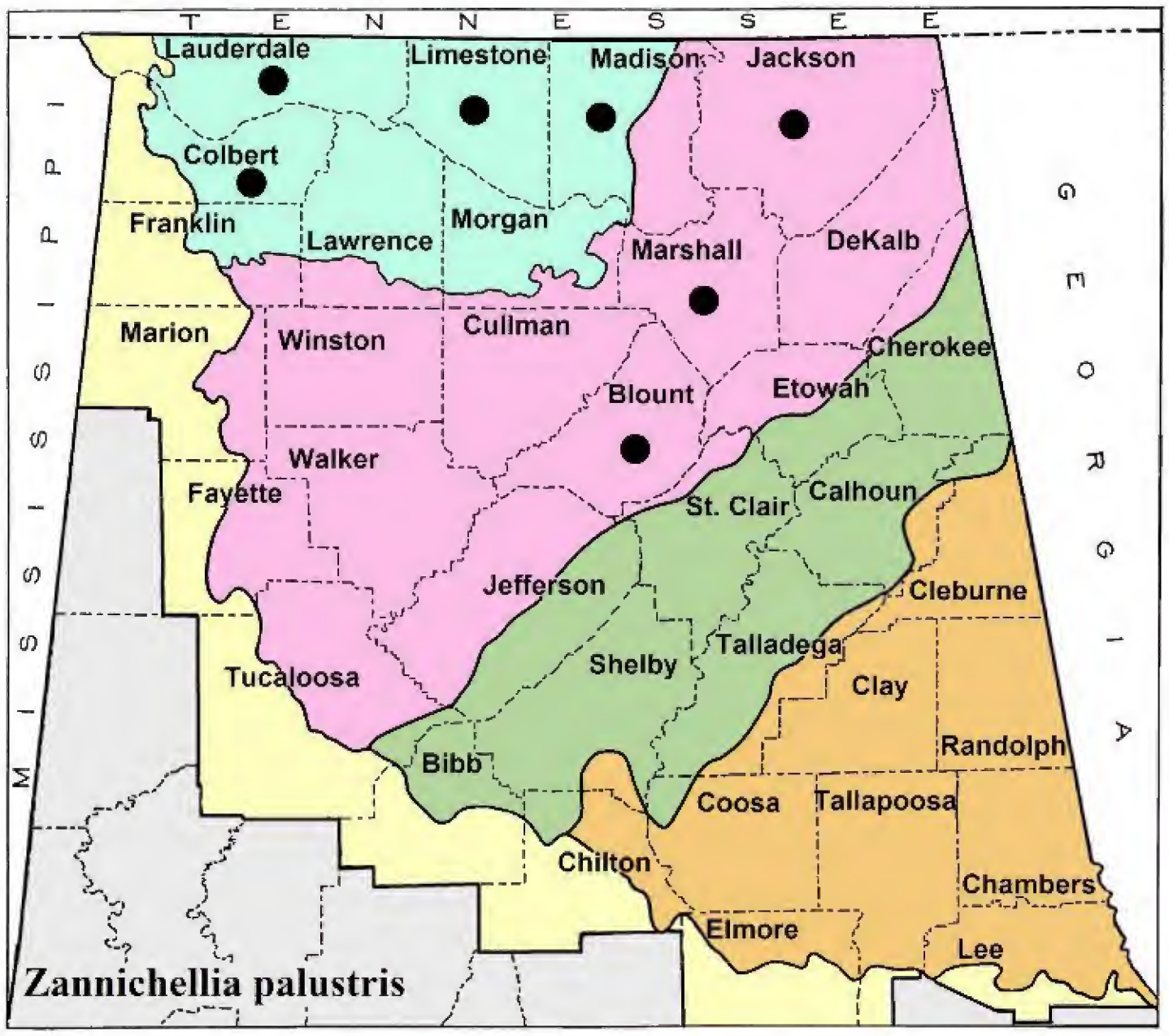


Figure 182. Distribution of *Zannichellia palustris* in northern Alabama.

Figure 183. *Zannichellia palustris*, Lower Saxony, Germany, 18 Sep 2012. Photo: Christian Fischer.

(184a) Axillary clusters of fruits. (184b) Close-up of dried fruits.

Figure 184. *Zannichellia palustris*, Lower Saxony, Germany, 18 Sep 2012. Photo: Christian Fischer. B. VDB, *Dennis & Price 2108*, 9 May 1979. Photo: Dan Spaulding.

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A MULTIVARIATE MORPHOMETRIC ANALYSIS OF THE *SOLIDAGO ULIGINOSA* COMPLEX (ASTERACEAE: ASTEREAE; *SOLIDAGO* SUBSECT. *MARITIMAE*) IN EASTERN NORTH AMERICA

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ABSTRACT

A multivariate morphometric study of the *Solidago uliginosa* complex of *Solidago* subsect. *Maritimae* was conducted to assess the morphological differences among *Solidago austrina* as "outgroup," *S. simulans*, and *S. uliginosa* (including *S. humilis*, *S. klughii S. linoides, S. neglecta*, *S. purshii*, *S. terrae-novae*, and *S. uniligulata*). An analysis of a matrix of 320 specimens by 37 traits of subsect. *Maritimae* was performed initially, then multiple analyses of the *S. uliginosa* complex with species limits defined in multiple ways to assess which taxa should be recognized and at what taxonomic rank within the *S. uliginosa* complex. Support was found for recognizing *S. simulans* and *S. uliginosa* and for recognizing 3 varieties within *S. uliginosa*: var. *uliginosa*, var. *peracuta, and* var. *terrae-novae*. A key to all species in *Solidago* subsect. *Maritimae* is included.

The *Solidago uliginosa* Nutt. complex consists of one to several species and multiple varieties, but with a tortuous history of names applied to them. Regardless of the names applied, the plants are all native to bogs and wet soils in eastern Canada and the northern midwest and northeastern regions of the U.S. and further south mostly at higher elevations in the Appalachian Mountains. All have lowest stem leaves with petioles sheathing the stem and blades that are lanceolate and finely to coarsely serrate on the margins. Sheathing lower stem leaves are found only in *S.* subsect. *Maritimae* (Torr. & Gray) Nesom, which includes the following 13 species accepted by Semple (2019): *S. austrina* Small, *S. azorica* Hochstetter ex Seubert, *S. chrysopsis* Small, *S. gracillima* Torr. & Gray, *S. maya* Semple, *S. mexicana* L., *S. paniculata* DC., *S. pulchra* Small, *S. sempervirens* L., *S. simulans* Fern., *S. stricta* Ait., *S. uliginosa*, and *S. virgata* Michx. Multiple species include more than one ploidy level. Only *S. uliginosa* sensu lato and *S. simulans* are viewed here as being part of the *S. uliginosa* complex, with *S. austrina* being included for comparison. Previously published multivariate morphometric studies were presented on the *S. sempervirens* complex (Semple et al. 2016a) and the *S. stricta* complex (Semple et al. 2016b). Details of the cytogeography of all species will be described in a paper now in preparation and information on chromosome numbers will only be referenced in this paper when pertinent to presentation of morphological variation.

Multiple species have been described within the *Solidago uliginosa* complex over the past two centuries. Formal nomenclatural information is provided in Table 1. *Solidago humilis* Banks ex Pursh is the oldest name for what is treated here as *S. uliginosa* Nutt. but is a later homonym and was long rejected as the valid name for the species. Torrey and Gray (1842) proposed the names *S. neglecta* Torr. & Gray and *Solidago linoides* Torr. & Gray for the more southern members of the complex with secund inflorescences with spreading inflorescence branches. These more southern plants are known to be tetraploid (Beaudry & Chabot 1959; Beaudry 1963, 1969; Morton 1981; Semple et al. 1981, 1984, 1993, 2015, 2019; Chmielewski et al. 1987). Torrey and Gray (1842) treated the northern non-secund members of the complex under the misapplied name *S. stricta* Ait.

listing *S. uliginosa* as a synonym. Semple (2013) noted that the name *S. stricta* was correctly applied to the New Jersey to North Carolina hexaploid species that is part of the *S. stricta/S. virgata* complex in *S.* subsect. *Maritimae* (Semple et al. 2016b). *Solidago purshii* Porter was proposed as a new name to replace *S. humilis* with the same type specimen, and this was adopted by some botanists subsequently (e.g. Britton 1901, Fernald 1950; Beaudry et al. 1958). Cronquist (1947) discussed application of the names *S. uliginosa*, *S. neglecta*, *S. linoides*, and *S. uniligulata*, and he concluded that all applied to the same species with the oldest valid name being *S. uliginosa*.

Cronquist (1947) concluded that two varieties could be recognized within *Solidago uliginosa*: plants of var. *uliginosa* have a secund inflorescence, usually with long ascending-diverging lower branches (Figs. 1-2), while plants of *S. uliginosa* var. *peracuta* (Fern.) Friesner have non-secund inflorescences with lower branches that are either relatively short or if longer than ascending and not strongly diverging (Fig. 3-4). The epithet *peracuta* refers to the sharply acute leaf apices that Fernald emphasized in protologue. In 1946, Cronquist annotated the holotype of var. *peracuta* with the following: "I take this to be merely a young form of what has passed as *S. uliginosa* Nutt.. The type of the latter, however, is the plant which has secund inflorescence and has passed as *S. uniligulata* or *S. neglecta.*" Plants with intermediate inflorescence traits occur.

Semple and Cook (2006) used the name *Solidago uliginosa* following Cronquist's application but did not recognize any varieties. Both var. *uliginosa* and var. *peracuta* include small to large shoots with smaller shoots being more common in the more northern portion of the range of distribution of the species. Stem height and the size of the inflorescence is strongly influenced by growing conditions and the length of the growing season. Rootstocks with very tall shoots in the field usually yielded only small shoots when transplanted to the greenhouse in confining pots, particularly after being in the greenhouse for more than one year.

Table 1. Species and variety names of taxa proposed in the *Solidago uliginosa* complex.

Solidago humilis Banks ex Pursh, Fl. Sept. 1814. non Mill. (1768), nec Desf. (1829). *Solidago virga-aurea* L. var. *humilis* (Banks ex Pursh) A. Gray, Man. (ed.2) 202. 1856. **TYPE**: **CANADA**. **Newfoundland**. 1766, *Banks s.n.* (holotype: BM.!, annotated by A. Gray 1881 "The original of mss Solander (the No. 1 added subsequently)."

Solidago uliginosa Nutt., J. Acad. Sci. Phila. 7: 101. 1834. **TYPE**: **USA**. **New Jersey**. *C. Pickering s.n.* (holotype: PH!).

Bigelowia uniligulata DC., Prodr. 5: 329. 1836. *Chrysoma uniligulata* (DC.) Nutt., Trans. Amer. Phil. Soc. n.s. 7: 325. 1841. *Solidago neglecta* Torr. & Gray var. *uniligulata* (DC.) B.S.P., Prelim. Cat. N. Y. Pl. 26. 1888. *Solidago uniligulata* (DC.) Porter, Mem. Torr. Bot. Club 5: 320. 1894. **TYPE**: "in Nova-Caesarea [=**New Jersey**], in arenosis a Virginia ad Carolina", s.d., *Greene s.n.*, (holotype: GDC jStor image g00455985!).

Solidago neglecta Torr. & A. Gray, Fl. N. Amer. 2(2): 213. 1842. *Solidago uniligulata* Pursh var. *neglecta* (Torr. & Gray) Fern., Rhodora 23: 292. 1922. **LECTOTYPE** (designated here): **Massachusetts**. Essex Co.: Ipswich, *Oakes s.n.* (NY!: isolectotype: GH!). The protologue alluded to a group of collections: "In swamps, Massachusetts! and New York! to North Carolina! and Indiana! Aug.-Sept." Other syntypes are these: **Massachusetts**. *Chapman s.n.* (NY!). **New York**. Staten Is., Aug 1841, *Torrey s.n.* (NY!); Island of New York, Aug 1841, *Torrey s.n.* (NY!). **North Carolina**. *Curtis s.n.* (NY!). **Ohio**. Columbus, *Lapham s.n.* (NY!).

Solidago linoides Torr. & A. Gray, Fl. N. Amer. 2: 216. 1842. *Solidago neglecta* Torr. & Gray var. *linoides* (Torr. & Gray) A. Gray, Syn. Fl. N. Amer. 1, pt. 2: 154. 1884. *Solidago uliginosa* Nutt. var. *linoides* (Torr. & Gray) Fern., Rhodora 49: 296. 1947. **TYPE**: **USA. New Jersey**. Wading River, pine barrens, sphagnous swamp, Sep 1833, *A. Gray s.n.* (holotype: GH!).

Solidago humilis Banks ex Pursh var. *microcephala* Porter, Bull. Torrey Bot. Club 19: 129. 1892. **TYPE**: **USA. Maine**. Mt. Desert Island, Frenchman's Camp Road, Aug. 1891, *Redfield s.n.* (holotype: not seen); "very small heads for species, scarcely a line and a half long" in protologue is of uncertain application. The holotype was not found at GH or PH.

Solidago purshii Porter, Bull. Torrey Bot. Club 21: 311. 1894. **TYPE: CANADA**. **Newfoundland**. 1766, *Banks s.n.* (holotype: BM!).

Solidago klughii Fern. [Rhodora 17: 5 1915. **TYPE**: **CANADA**. **Ontario**. Bruce Co.: Oliphant, 14 Aug 1905, *A.B. Klugh 3* (holotype: GH!).

Solidago humilis Banks ex Pursh var. *peracuta* Fern., Rhodora 17: 6. 1915. *Solidago uliginosa* Nutt. var. *peracuta* (Fern.) Friesner, Butler Univ. Bot. Studies 3, no. 1: 55. 1933. **TYPE**: **CANADA**. **Newfoundland**. East Branch of Humber R., Middle Birchy Pond, open rocky woods, 13 Jul 1910, *Fernald & Wiegand 4097* (holotype: GH!).

Solidago uniligulata DC. var. *levipes* Fern., Rhodora 17: 7. 1915. *Solidago uliginosa* Nutt. var. *levipes* (Fern.) Fern., Rhodora 49: 296. 1947. **TYPE**: **USA. New York**. Penn Yan, *Sartell s.n.* (holotype: GH!).

Solidago simulans Fern., Rhodora 38: 205. 1936. **TYPE**: **USA. North Carolina**. Macon Co.: near Highlands, moist rocks on the high mountains, 15 Sep 1897, *Biltmore Herb. 5730* (holotype: GH!; isotypes: NY!, US online image!).

Solidago simulans Fern. [Rhodora 38: 205. 1936. **TYPE**: **USA. North Carolina**. Macon Co.: near Highlands, moist rocks on the high mountains, 15 Sep 1897, *Biltmore Herb. 5730* (holotype: GH!; isotypes: NY!, US online image!).

Solidago humilis Banks ex Pursh var. *abbei* Boivin, Nat. Canad. 89: 73. 1962. **TYPE**: **CANADA**. **Québec**. Ungava, mainland south of Cairn Island, abundant in a wet, mossy and grassy spruce bog in the hills, 9 Aug 1939, *E.C. Abbe 3761* (holotype: DAO, not seen: isotype: MIN jStor image!).

Solidago humilis Banks ex Pursh var. *microcephala* Porter, [Bull. Torrey Bot. Club 19: 129. 1892. **TYPE**: **USA**. **Maine**. Mt. Desert Island, Frenchman's Camp Road, Aug. 1891, *Redfield s.n.* (holotype: not found); "very small heads for species, scarcely a line and a half long" in protologue] is of uncertain application. This is the oldest varietal name in the *S. uliginosa* complex and thus has priority and a new combination would be required under *S. uliginosa* if the holotype collection is located and found to be the same taxon as of *S. ulignosa* var. *peracuta*.

Solidago klughii Fern. was compared in the protologue to *S. guiradonis* A. Gray in phyllary and leaf traits. *Solidago guiradonis* is a member of *S.* subsect. *Junceae* and is a rare endemic in California and a close relative of *S. confinis* Nutt. and *S. spectabilis* (D.C. Eaton) A. Gray (Semple and Cook 2006; Semple 2019). In his annotation on the type specimen Cronquist in 1946 hypothesized that *S. klughii* was "only a phase of *S. uliginosa* var. *peracuta* (Fern.) Friesn." *Klugh 3* (GH) has sheathing basal leaf bases and linear leaves. Similar plants are known to be tetraploid in the bogs on the west side of the Bruce Peninsula in Ontario; e.g., *Semple & K. Shea Semple 2451* (WAT, CAN, MO, USF), reported in Semple et al. (1981) and included in the multivariate analyses below.

Two additional published names appear to be either minor variants or immature plants of *Solidago uliginosa*: (1) The holotype of *Solidago uniligulata* DC. var. *levipes* Fern. has large serrations on the narrowly oblanceolate to lanceolate lower leaves and a narrow, elongated inflorescence with immature heads. Fernald (1950) keyed the variety out as having "pedicels glabrous or glabrous and glutinous" and noted that plants came from "Bogs and wet sands centr. N.Y. to s. Ont." (2) *Solidago humilis* var. *abbei* Boivin was based on small shoots (30-33 cm) with few heads. Such diminutive shoots are frequent in northern collections of the *S. uliginosa* complex and not distinct from other northern collections seen. Both names belong in synonymy under var. *peracuta*.

The southernmost member at species rank of the *S. uliginosa* complex and most recently described is *S. simulans* Fern. As originally circumscribed, the species was limited to plants of the high mountains of Macon Co., North Carolina, in the southern Appalachian Mts. (Fig. 7), where it has been observed growing in shallow soil of seepage on exposed rock faces (Fig. 8). In the protologue, Fernald compared the species to *S. uliginosa* and *S. austrina* Small. The species can have some of the largest basal rosette leaves observed in the field of all species in the *S. uliginosa* complex (Fig. 9).

Shoots are similar to those of typical *S. uliginosa*. Cronquist (1980) included the species in a broadly defined *S. gracillima* Torr. & A. Gray and noted that *S. simulans* was "a broad-leaved extreme, approaching *S. uliginosa.*" Semple and Cook (2006) treated *S. simulans* in synonymy under *S. uliginosa* but noted that it "might warrant recognition as a narrowly distributed endemic." Semple (2012) selected a lectotype for *S. gracillima* that effectively restricted that species to plants of the *S. stricta*/*S. virgata* complex with a few long to very long lower inflorescence branches, thereby excluding *S. simulans* from *S. gracillima*. *Solidago simulans* belongs in the *S. uliginosa* complex.

The ranges of distribution of *Solidago austrina*, *S. simulans* and *S. uliginosa* and locations of samples included in the multivariate analyses are shown in Fig. 10. *Solidago austrina* is the most southern of the three species occurring along the outer margins of the Piedmont from North Carolina to Alabama with populations extending north through eastern Tennessee to southern Kentucky and south into Panhandle Florida. As delimited here, *S. simulans* occurs in scattered locations on the Piedmont in North Carolina and at generally higher elevations in the Appalachian Mts. of northeastern Georgia, western North Carolina and eastern Tennessee and adjacent southwestern Virginia. *Solidago uliginosa* occurs over much of eastern North America from Newfoundland and Labrador to Hudson's Bay and southeastern Manitoba south to north central Illinois and New Jersey, Maryland and West Virginia, and scattered locations in Virginia in the mountains and further east in a range of boggy and marshy habitats (Fig. 10).

Numerous chromosome number reports have been published for taxa in *Solidago* subsect. *Maritimae*, including diploids 2*n*=9II or 2n=18, tetraploids 2*n*=18II or 2*n*=36, and hexaploids 2*n*=54. The cytogeography and a review of published chromosome counts will be presented in detail in a separate paper currently in preparation by the first author and Rachel Cook.

A multivariate analysis of 105 specimens of *S. austrina*, *S. simulans*, and *S. uliginosa* was undertaken to investigate the levels of similarities among taxa and to determine which traits most strongly differentiated these species and possible varieties within *S. uliginosa*. This has not been done previously. Specimens of *S. austrina* were included because the species can be similar to some morphs of *S. uliginosa*, although the latter have fewer leaves on the stems. Statistically supported answers to the following questions were the goals of the investigation: How many species should be recognized in the *S. uliginosa* complex? How many varieties, if any, should be recognized within *S. uliginosa* itself? Which traits are best at separating the taxa supported by the analyses?

MATERIAL AND METHODS

Herbarium specimens of *Solidago austrina*, *S. simulans*, and the *S. ulignosa* complex were borrowed and examined from the following herbaria (BRIT, FLAS, FSU, GA, GH, the J.K. Morton personal herbarium now in TRT, KYU, MT, NCU, NY, USCH, and WAT in MT; Thiers continuously updated). Digital images posted online by the following herbarium via the SouthEast Regional Network of Expertise and Collections (SERNEC Data Portal 2019) were examined to map distributions: ABLC, APSC, ASC, BHO, BRU, BUT, CALVIN, CLEMS, CMC, EMC, F, FSU, HUNT, ILL, IND, LSU, LYN, MCA, MICH, MIN, MOR, MSC, MUH, NO, NY, OSU, PH, UNC, UWL, VPI, WIS. Of the several thousand specimens examined, 105 were chosen and measured for the statistical analyses based on completeness of the specimen, state of maturity, and geographical distribution. In total, 20 vegetative and 17 floral traits were scored for the final analyses (Table 2). Additional stem, leaf, inflorescence, and phyllary indument traits were used in assigning specimens to a priori groups.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016a) and are not repeated here. Eleven analyses were performed. In the first analysis, *S. austrina* (40 specimens), *S. azorica* (17 specimens), *S. chrysopsis* (19 specimens), *S.*

Figure 1. A robust shoot of tetraploid *Solidago uliginosa* var. *uliginosa*, *Semple & Suripto 5014* (WAT) from Mackinac Co., Michigan.

Figure 2. A robust shoot of tetraploid *Solidago uliginosa* var. *uliginosa*, *Semple & Suripto 9524* (WAT) from Ocean Co., New Jersey; very long inflorescence branches.

Figure 3. Robust shoots of diploid *Solidago uliginosa var. peracuta*, *Semple & Keir 4602* (WAT) from Wolfe Co., Québec.

Figure 4. Small shoots of *Solidago uliginosa* var. *peracuta*, *Gagnon 74499* (MT) from Lac Nahalie in northwestern, Québec.

Figure 5. *Solidago uliginosa* var. *terrae-novae*, *Rouleau 5165* (MT) from the Avalon Peninsula, Newfoundland.

Figure 6. *Solidago uliginosa* var. *terrae-novae*, *Rouleau 5900* (MT) from Newfoundland.

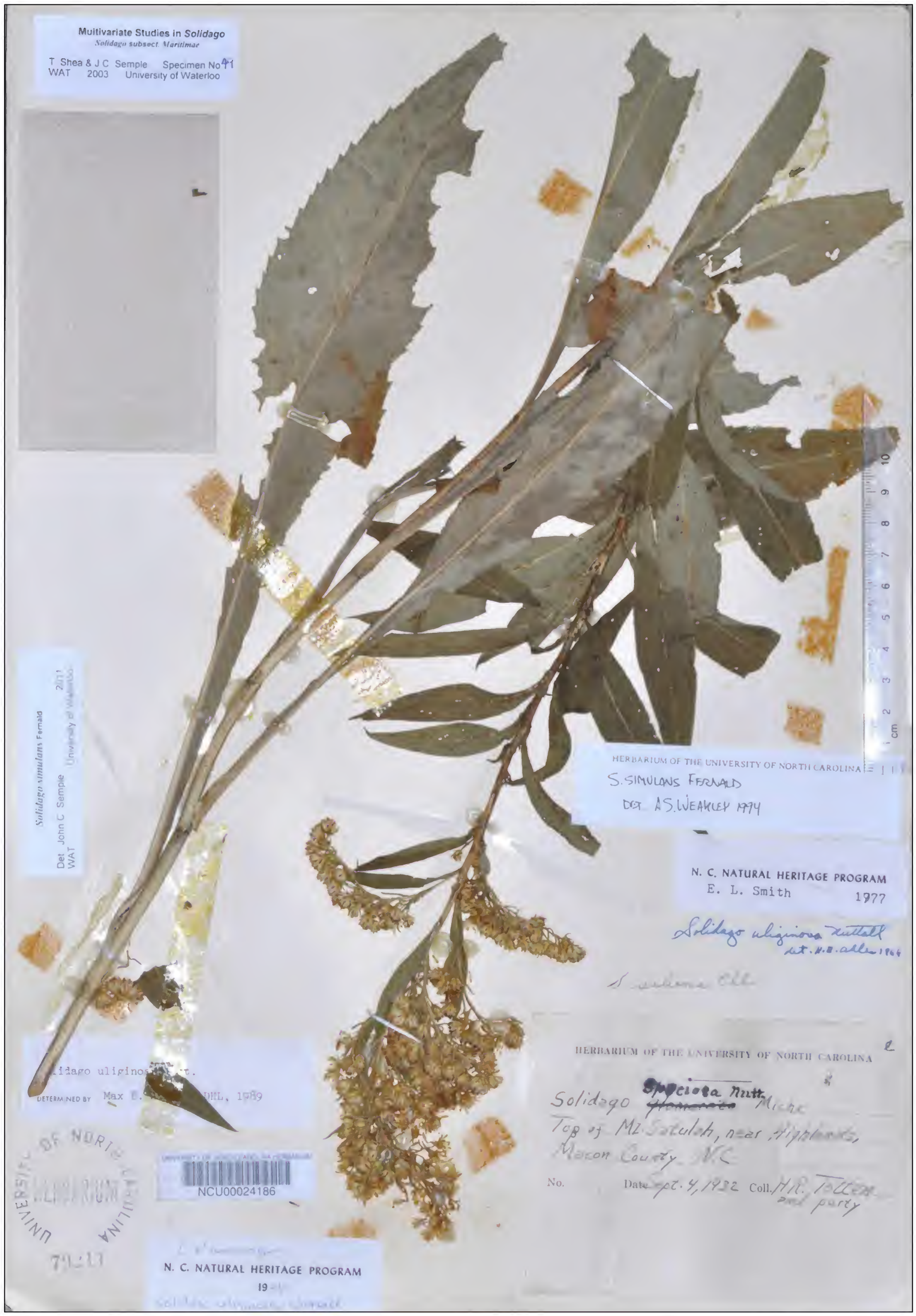

Figure 7. *Solidago simulans*, *Totten and party s.n.* (NCU) from Satulah Mt., Macon Co., North Carolina.

Figure 8. *Solidago simulans*, Whiteside Mt., Jackson Co., North Carolina.

Figure 9. *Solidago simulans*, basal rosettes, Whiteside Mt., Jackson Co., North Carolina.

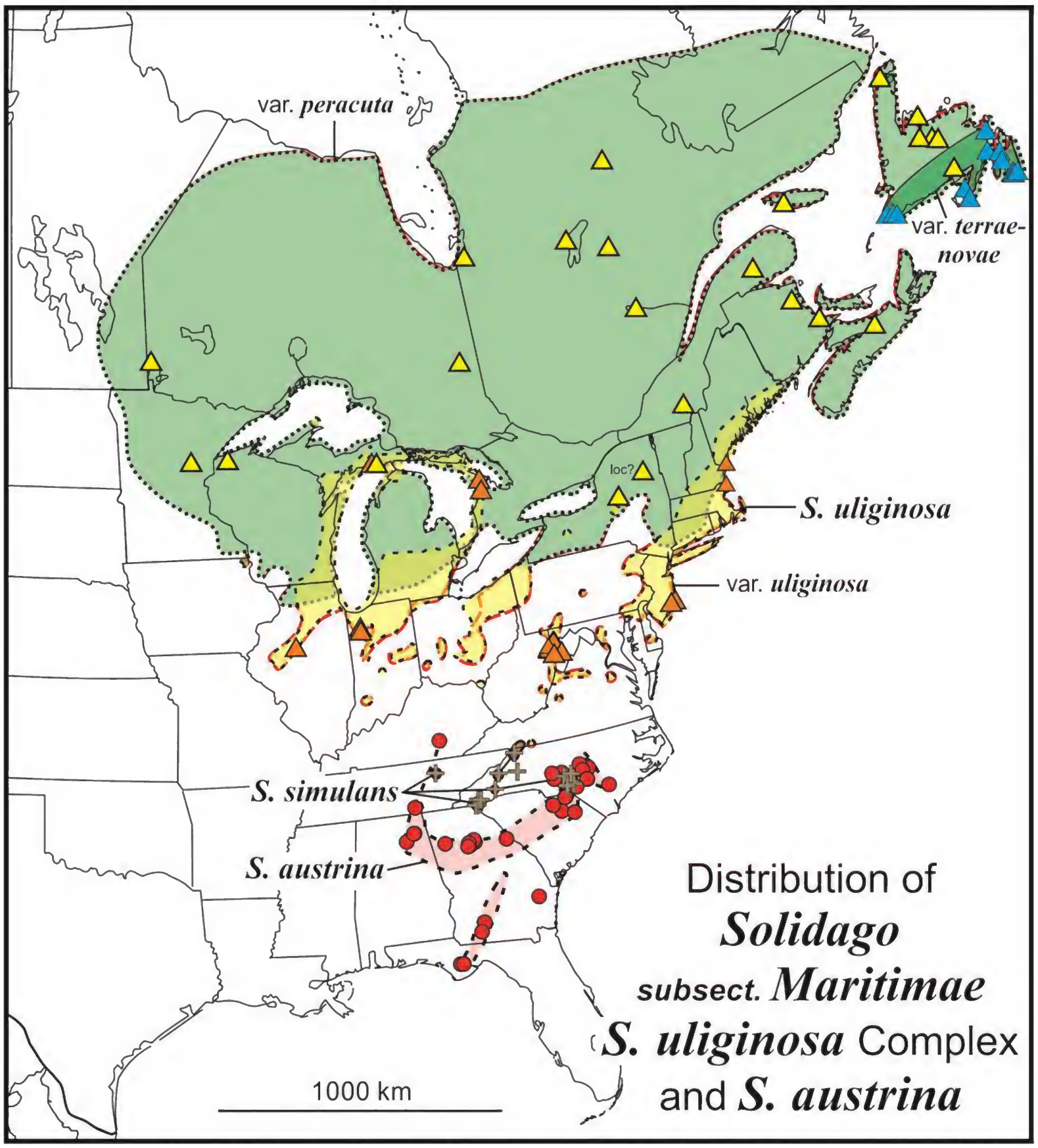

Figure 10. Ranges of distribution and source locations of multivariate samples in eastern North America of *Solidago austrina* (red dots), *S. simulans (brown +s), and S. uliginosa* (var. *uliginosa* s.l., orange triangles, mostly or exclusively tetraploid; var. *peracuta/"purshii",* yellow triangles (mostly diploid); var. *terrae-novae,* light blue triangles); ranges of varieties based on conclusions drawn from the multivariate analyses and examination of online images of herbarium specimens.

S. gracillima (18 specimens), *S. maya* (9 specimens), *S. mexicana* (45 specimens), *S. paniculata* (13 specimens), *S. pulchra* (15 specimens), *S. sempervirens* (16), *S. simulans* (16 specimens), *S. stricta* (34 specimens), *S. uliginosa* (47 specimens), and *S. virgata* (29 specimens) were included in a STEPWISE discriminant analysis and then a COMPLETE discriminant analysis with seven traits because only eight specimens of *S. maya* could be included. In the second analysis, *S. austrina*, *S. simulans*, and *S. uliginosa* s.l. were included in a STEPWISE discriminant. In the third analysis, *S. austrina* and *S. ulginosa* s.l. were included in a STEPWISE discriminant. In the fourth analysis, *S. austrina* and *S. ulginosa* s.s. were included in a STEPWISE discriminant. In the fifth analysis, *S. austrina, S. purshii* (including *var. peracuta* and var. *terrae-novae*), *S. simulans*, and *S. uliginosa* s.s. were included in a STEPWISE analysis. In the sixth analysis, *S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* (including var. *peracuta* and var. *uliginosa*) were included in a STEPWISE discriminant analysis. In

the seventh analysis, *S. austrina*, *S. purshii*, *S. simulans*, S. *terrae-novae*, and *S. uliginosa* s.s. were included in a STEPWISE discriminant analysis. In the eighth analysis, *S. purshii*, *S. terra-novae*, and *S. uliginosa* s.s. were included in a STEPWISE discriminant analysis. In the ninth analysis, *S. austrina*, *S. purshii*, S. *terrae-novae*, and *S. uliginosa* (including *S. simulans*) were included in a STEPWISE discriminant analysis. In the tenth analysis, *S. terrae-novae* and *S. uliginosa* (including *S. purshii*) were included in a STEPWISE discriminant analysis. In the eleventh analysis, *S. purshii* and *S. terrae-novae* were included in a STEPWISE discriminant analysis. Numerous additional preliminary analyses were run over multiple years as the sample sizes of the taxa were increased but are not reported here. Specimens of *Solidago austrina* were included as an a priori group for comparative purposes in the multiple analyses of the *S. uliginosa* complex.

Table 2. Traits scored for the multivariate analyses of 320 specimens of *Solidago* subsect. *Maritimae*.

Abbreviation	**Description of trait scored**
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
CAPBRNLN	Length of lower inflorescence branches (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLLN	Outer phyllary length (mm)
MIDPHYLLN	Mid series phyllary length (mm)
MIDPHYLWD	Mid series phyllary width at widest point (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)

DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DACHPUB	Number of hairs on disc floret ovary/fruit body
UPSTMNOD25	Number of nodes in the top 25% of the stem below the inflorescence
UPSTMNOD20	Number of nodes in the top 20% of the stem below the inflorescence

RESULTS

Analysis 1: Thirteen species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length, width, and number of margin serrations. Basal rosette leaves were often not present and were not included in the analyses. Lower stem leaves were present on many specimens but were not included in the analyses because their traits correlated highly among themselves and with mid and upper stem leaf traits. Among the floral traits scored, only ray floret pappus length and disc floret pappus length correlated highly; the former was included in the analyses. The numbers of nodes in the top 25% and 20% of the stem were highly correlated and only the number of nodes in the top 25% of the step were included in the analysis.

In the COMPLETE discriminant analysis of 320 specimens of 13 species level a priori groups (*Solidago austrina*, *S. azorica*, *S. chrysopsis*, *S. gracillima*, *S. maya*, *S. mexicana*, *S. paniculata*, *S. pulchra*, *S. sempervirens*, *S. simulans*, *S. stricta*, *S. uliginosa*, and *S. virgata*), the following seven of ten traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: length of the longest inflorescence branches (43.26), mid stem leaf width (27.54), mid stem leaf length (18.99), ray floret pappus length (16.91), number of disc florets (16.34), number of mid stem leaf margin serrations (13.74), and mid series phyllary width (32.07). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 3. F-values based on Mahalanobis distances of the between group centroids indicated the that largest separations were between *S. gracillima* and *S. mexicana* (77.963), *S. gracillima* and *S. uliginosa* (77.914), and *S. gracillima* and *S. sempervirens* (75.558); the smallest separations were between *S. maya* and *S virgata* (1.761), *S. chrysopsis* and *S. maya* (2.865), *S. simulans* and *S. uliginosa* (3.116), and *S. maya* and *S. stricta* (3.132).

In the Classificatory Discriminant Analysis of 320 specimens of the 13 species level a priori groups (*Solidago austrina*, *S. azorica*, *S. chrysopsis*, *S. gracillima*, *S. maya*, *S. mexicana*, *S. paniculata*, *S. pulchra*, *S. sempervirens*, *S. simulans*, *S. stricta*, *S. uliginosa*, and *S. virgata*), percents of correct a posterori assignment to the same a priori group ranged from 44-89%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results are presented in order of decreasing percents of correct placement. Percents of correct a posteriori assign to the same a priori group ranged from 84-89% for *S. chrysopsis*, *S. gracillima*, *S. pulchra*, and *S. paniculata*. Percents of correct a posteriori assign to the same a priori group ranged from 75-77% for *S. azorica*, *S. simulans*, and *S. virgata*. Percents of correct a posteriori assign to the same a priori group were 69% for *S. sempervirens*, 56% for *S. stricta*, 53 percent for *S. uliginosa*, 50% for *S. austrina*, 44% for *S. maya*, and 38% for *S. mexicana*. The results are not discussed further.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 320 specimens of 13 species of *Solidago* subsect. *Maritimae* are presented in Fig. 11. Eigenvalues on the seven axes were 2.744, 1.861, 1.016, 0.880, 0.538, 0.327, and 0.028. Only symbols for *S.*

Table 3. Between groups F-matrix for the 13 a priori group analysis of *S.* subsect. *Maritimae* (df = 10 288).

Group	***austrina***	***azorica***	***chrysopsis***	***gracillima***	***maya***	***mexicana***	***paniculata***	***pulchra***	***sempervirens***
azorica	43.155								
chrysopsis	13.922	50.723							
gracillima	63.067	96.655							
maya	4.130	25.362	56.681						
mexicana	14.455	46.667	2.865	32.694					
paniculata	24.131	44.949	8.747	77.963	0.661				
pulchra	10.708	47.036	17.871	45.193	5.520	8.895			
sempervirens	23.198	18.558	13.733	57.054	7.941	16.579	24.845		
simulans	8.572	20.277	29.280	75.558	9.224	13.245	11.047	24.635	
stricta	12.664	47.387	20.647	52.739	7.831	15.701	19.867	25.163	13.580
uliginosa	19.958	41.461	14.378	59.225	3.132	15.149	17.212	20.237	23.826
virgata	11.263	53.233	25.730	77.914	10.165	29.062	26.638	38.915	26.972

Group	***simulans***	***stricta***	***uliginosa***
stricta	15.232		
uliginosa	3.116	35.894	
virgata	16.261	6.051	30.039

Wilks' lambda = 0.0117 df = 7 12 307; Approx. F= 23.4956 df = 84 1851 prob = 0.0000

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of 13 a priori groups; a posteriori placements to groups in rows.

Group	***austrina***	***azorica***	***chrysopsis***	***gracillima***	***maya***	***mexicana***	***paniculata***	***pulchra***	***sempervirens***	***simulans***	***stricta***	***uliginosa***	*virgata*	**% correct**
austrina	20	0	2	1	0	4	0	3	0	3	3	2	2	50
azorica	0	13	0	0	0	0	0	0	0	0	0	0	0	76
chrysopsis	0	0	17	0	1	0	0	0	0	0	0	0	1	89
gracillima	1	0	0	17	1	0	0	0	0	0	0	0	0	89
maya	0	0	0	0	4	3	0	0	0	0	0	0	2	44
mexicana	1	1	1	0	11	17	4	1	3	2	2	1	3	38
paniculata	0	0	0	0	1	1	11	0	0	0	0	0	0	85
pulchra	1	0	0	0	0	0	0	13	0	0	0	0	1	87
sempervirens	0	0	0	0	2	0	2	0	11	0	0	1	0	69
simulans	1	0	0	0	0	1	0	0	0	13	0	2	0	75
stricta	4	0	2	0	2	0	0	0	0	1	19	0	7	56
uliginosa	4	1	0	0	2	5	0	0	0	11	0	32	0	53
virgata	2	0	3	0	1	0	0	0	0	0	1	0	23	77
Totals	34	15	25	18	25	31	17	17	14	28	25	38	39	63

Jackknifed classification matrix

Group	*austrina*	*azorica*	*chrysopsis*	*gracillima*	*maya*	*mexicana*	*paniculata*	*pulchra*	*sempervirens*	*simulans*	*stricta*	*uliginosa*	*virgata*	% correct
austrina	17	0	2	1	0	5	0	4	0	3	3	3	2	43
azorica	0	13	0	0	0	0	0	0	0	4	0	0	0	46
chrysopsis	1	0	16	0	0	0	0	0	0	0	0	0	2	84
gracillima	1	0	0	16	1	0	0	0	0	0	1	0	0	84
maya	0	0	1	0	2	4	0	0	0	0	0	0	2	22
mexicana	1	1	2	0	10	16	4	1	4	1	2	0	3	36
paniculata	0	0	0	0	1	2	10	0	0	0	0	0	0	77
pulchra	1	0	0	0	0	0	0	13	0	0	0	0	1	87
sempervirens	0	1	0	0	2	0	2	0	10	0	0	1	0	63
simulans	3	0	0	0	0	1	0	0	0	9	0	3	0	56
stricta	4	0	2	0	2	0	0	0	0	0	18	0	8	53
uliginosa	4	1	0	0	2	6	0	0	0	11	0	23	0	49
virgata	2	0	3	0	1	0	0	0	0	0	1	0	23	77
Totals	34	16	26	17	21	34	16	18	14	28	25	30	41	58

gracillima were separated from symbols for other taxa. There was partial to complete overlap of symbols for all other species.

Analyses 2-10: the S. uliginosa complex

The Pearson correlation matrix for traits of specimens of *Solidago austrina*, *S. simulans*, and *S. uliginosa* included $r > |0.7|$ for most pairs of basal and lower leaf traits and mid and upper leaf traits reducing the number used to mid stem leaf length and the numbers of mid stem and upper stem leaf serrations. Basal rosette leaves were only sometimes present and were not included in the discriminant analyses. Only some floral traits were correlated. The following traits were included in all the subsequent STEPWISE analyses: length of the longest inflorescence branches, involucre height, mid series phyllary length and width, the numbers of ray and disc florets, the lengths of the ray floret lamina, ovary/fruit body, and pappus, the lengths of disc corolla, corolla lobes, fruit/ovary body, and pappus, and the number of nodes in the top 25% of the stem below the inflorescence.

Analysis 2: Three species level a priori groups analysis of the S. uliginosa complex

In the STEPWISE discriminant analysis of 105 specimens of three species level a priori groups *Solidago austrina*, *S. simulans* (including all specimens from northeastern Georgia, North Carolina, and Tennessee), and *S. uliginosa* (including all specimens from West Virginia north to northern Ontario, Québec and Newfoundland) the following six traits were selected and are listed in order of decreasing F-to-remove values: number of disc florets (42.78), number of ray florets (19.14), number of nodes in the top 25% of stem below the inflorescence (18.64), mid series phyllary length, (9.62), mid stem leaf length (6.35), and ray floret lamina length (6.06). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 5. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. uliginosa* (52.645); the smallest separation was between *S. simulans* and *S. uliginosa* (10.216).

In the Classificatory Discriminant Analysis of 105 specimens of the four species level a priori groups (*S. austrina*, *S. simulans*, and *S. uliginosa*), percents of correct a posteriori assignment to the same a priori group ranged from 87-88%. The Classification matrix and Jackknife classification

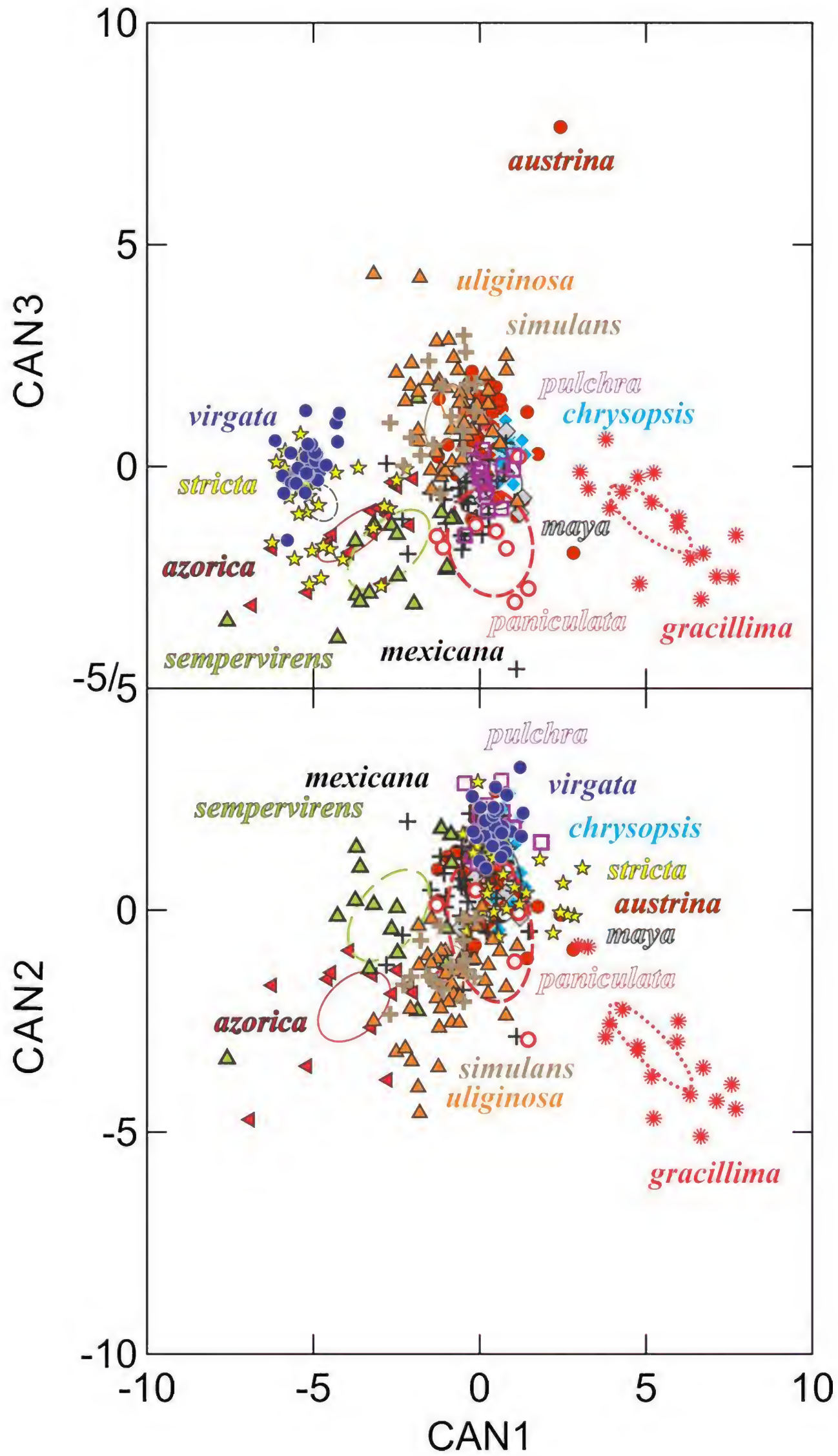

Figure 11. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 320 specimens in 13 a priori groups of the Solidago subsect. Maritimae from a seven-trait COMPLETE Analysis: *S. austrina* (red dots), *S. azorica* (left oriented red triangles), *S. chrysopsis* (blue diamonds), *S. gracillima* (red star bursts), *S. maya* (gray diamonds), *S. mexicana* (black +s), *S. paniculata* (red circles), *S. pulchra* (magenta squares), *S. sempervirens* (green triangles), *S. simulans* (brown +s), *S. stricta* (yellow stars), *S. uliginosa* (orange triangles), and *S. virgata* (dark blue dots).

matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. Fourteen of the 16 specimens of the *S. simulans* a priori group (88%) were assigned a posteriori into the *S. simulans* group; 7 specimens with 92-100% probability, 1 specimen with 72% probability, 1 specimen with 62% probability (287), and 1 specimens with 59% probability (*Godfrey 6949* GH from Scotland Co., North Carolina; originally identified by the collector as *S. uniligulata* var. *neglecta* and later annotated by M.L. Fernald in 1947 as *S. uliginosa*). Two specimens of the *S. simulans* a priori group were assigned to *S. uliginosa* with 80% probability (20% to *S. simulans*; *Chapman s.n.* NY from middle Florida; a problematic shoot that has a small inflorescence with short branches that is more like *S. uliginosa* but the provenance is much too far south for either species) and 79% probability (20% to *S. simulans*; *Semple 11590* WAT from Whiteside Mt., North Carolina; *Semple 11591* WAT from the same population was assigned to *S. simulans* with 89% probability; Fig. 6). Thirty-four of 39 specimens of the *S. austrina* a priori group (87%) plus 1 additional specimen only included a posteriori were assigned a posteriori into the *S. austrina* group; 32 specimens with 92-100% probability, 1 specimen with 72% probability, 1 specimen with 63% probability (*Heller 1284* NY from Rowan Co., North Carolina), and 1 specimen with 58% probability (*Semple & Suripto 9786* WAT a diploid from Clarendon Co., South Carolina). Five specimens of the *S. austrina* a priori group were assigned a posteriori to other species: 3 specimens to *S. simulans* with 90% probability (*Lindholm s.n.* GA from Liberty Co., Florida), 85% probability (*Lazor 4587* MT from Liberty Co., Florida), and 79% probability (*Radford 19485* NCU from Montgomery Co., North Carolina). Forty-one of 47 specimens of the *S. uliginosa* a priori group (87%) were assigned a posteriori into the *S. uliginosa* group; 28 specimens with 91-100% probability, 8 specimens with 81-89% probability, 3 specimens with 72-77%, 1 specimen with 66% probability (*Umbach s.n.* NCU from Indiana), and 1 specimen with 58% probability (*Downs 6769* NCU from West Virginia). Six specimens of the *S. uliginosa* a priori group were assigned a posteriori to *S. simulans* with 83% probability (*Semple & Suripto 9524* WAT from New Jersey; Fig. 2), 68% probability (*Chase 3386* USCH from Tazewell Co., Illinois), 67% probability (*Cusick 25744* NCU from West Virginia), 64% probability (*Bouchard et al. 92408* MT from Newfoundland; small shoot with a var. *peracuta*-like inflorescence), 56% probability (*Semple & Suripto* 9590 WAT from York Co., Maine; a robust shoot with a large inflorescence with long ascending spreading branches), and 50% probability (*Semple 11814* WAT from New Jersey).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 105 specimens of *Solidago austrina*, *S. simulans*, and *S. uliginosa* is presented in Fig. 12. Eigenvalues on the first two axes were 3.398 and 0.499.

Table 5. Between groups F-matrix for the four species level a priori groups analysis (df = 6 94).

Group	*austrina*	*simulans*
simulans	19.218	
uliginosa	52.645	10.216

Wilks' lambda = 0.1517 df = 6 2 99; Approx. F= 24.5629 df = 12 188 prob = 0.0000

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*austrina*	*simulans*	*uliginosa*	% correct
austrina	34	3	2	87
simulans	0	14	2	88
uliginosa	0	6	71	87
Totals	34	23	45	87

Jackknifed classification matrix

Group	*austrina*	*simulans*	*uliginosa*	% correct
austrina	34	3	2	87
simulans	1	12	3	75
uliginosa	0	6	41	87
Totals	35	21	46	85

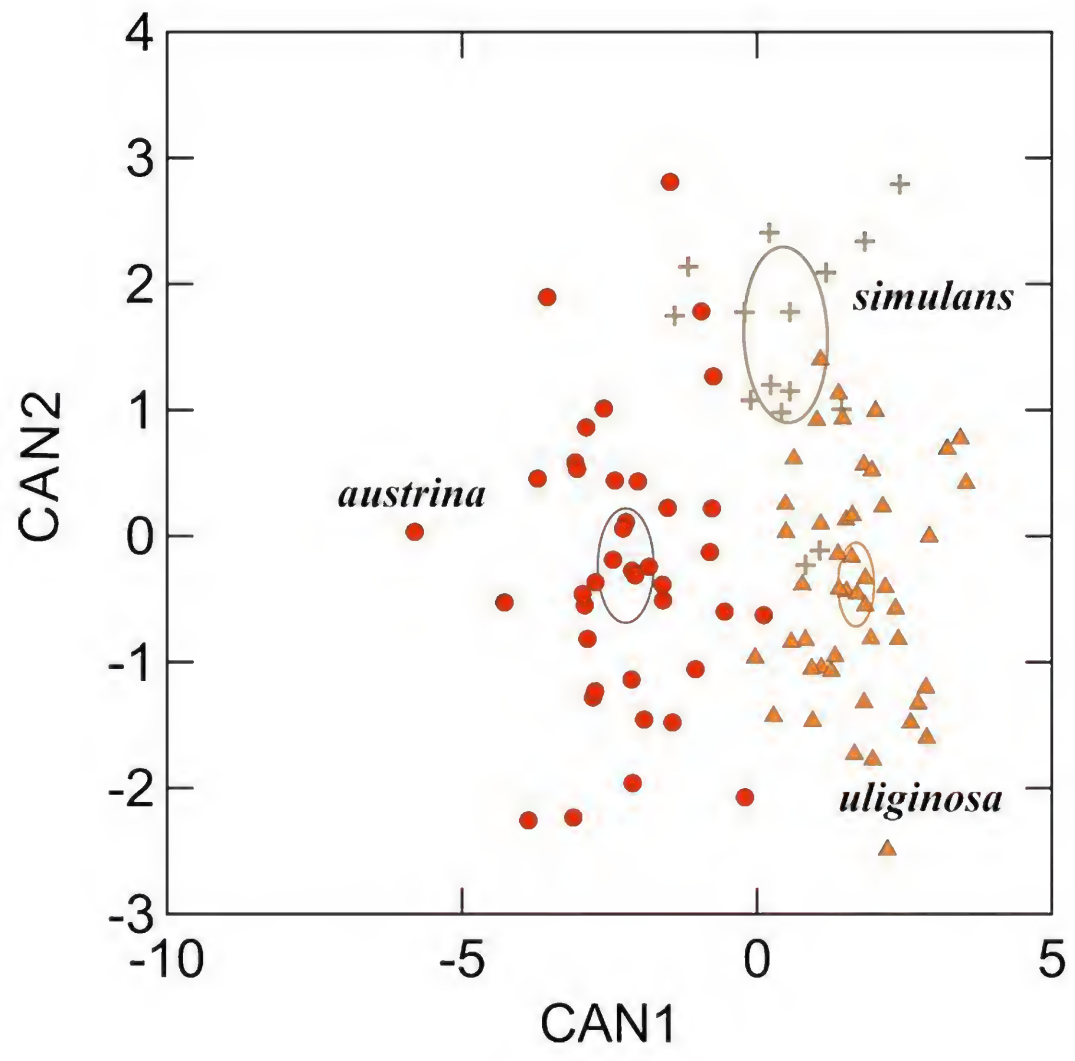

Figure 12. Plot of canonical scores (CAN1 vs CAN2) analysis for 105 specimens of *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. simulans* (brown +s), and *S. uliginosa* (orange triangles).

Analysis 3: Two species level a priori groups analysis: Solidago simulans and S. ulginosa s.l.

In the STEPWISE discriminant analysis of 63 specimens of two species level a priori groups (*S. simulans* and *S. uliginosa* including *S. purshii* and *S. terrae-novae*), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid series phyllary length (43.34), number of ray florets (15.79), number of nodes in the top 25% of stem below inflorescence (6.53), and length or the longest lower inflorescence branches (5.87). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago simulans* and *S. uliginosa* s.l. had an F-to separate value of 22.908 (Wilks' lambda = 0.3876 df = 4 1 61; Approx. F= 22.908 df = 4 58 prob = 0.0000).

In the Classificatory Discriminant Analysis of 63 specimens of the two species level a priori groups (*S. simulans* and *S. uliginosa* s.l.), percents of correct a posterori assignment to the same a priori group were 94% and 87%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Fifteen of the 16 specimens of the *S. simulans* a priori group (94%) were assigned a posteriori into the *S. simulans* group; 12 specimens with 90-100% probability, 1 specimen

with 88% probability, 1 specimen with 62% probability, and 1 specimen with 59% probability (*Semple 11590* WAT from Whiteside Mt., North Carolina; *Semple 11591* WAT from the same population was assigned to *S. simulans* with 100% probability; Fig. 6). One specimen of the *S. simulans* a priori groups were assigned to *S. uliginosa* with 79% (*Chapman s.n.* NY from middle Florida; a problematic specimen of uncertain identity and provenance). Forty of 47 specimens of the *S. uliginosa* s.l. a priori group (87%) were assigned a posteriori into the *S. uliginosa* s.l. group; 35 specimens with 94-100% probability, 4 specimens with 80-89% probability, and 1 specimen with 78% probability. Six specimens of the *S. uliginosa* s.l. a priori group were assigned to *S. simulans* with 80% probability (*Semple & Suripto 9524* WAT from New Jersey; a tetraploid, Fig. 2), 79% probability (*Cusick 25744* NCU from West Virginia), 72% probability (*Chase 3386* USCH from Tazewell Co., Illinois), 69% probability (*Semple 11814* WAT a tetraploid from Ocean Co., New Jersey), 54% probability (*Bouchard et al. 92408* MT from Newfoundland), and 54% probability (*Semple & Brouillet 3660* WAT from Oneida Co., New York; a 91 cm tall diploid).

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	*simulans*	*uliginosa*	% correct
simulans	15	1	94
uliginosa	6	41	87
Totals	21	42	89

Jackknifed classification matrix

Group	*simulans*	*uliginosa*	% correct
simulans	15	1	94
uliginosa	6	41	87
Totals	21	42	89

Histograms of canonical scores (CAN1) for *S. simulans* and *S. uliginosa* s.l. are shown in Fig. 13. The eigenvalue on the first axis was 1.580.

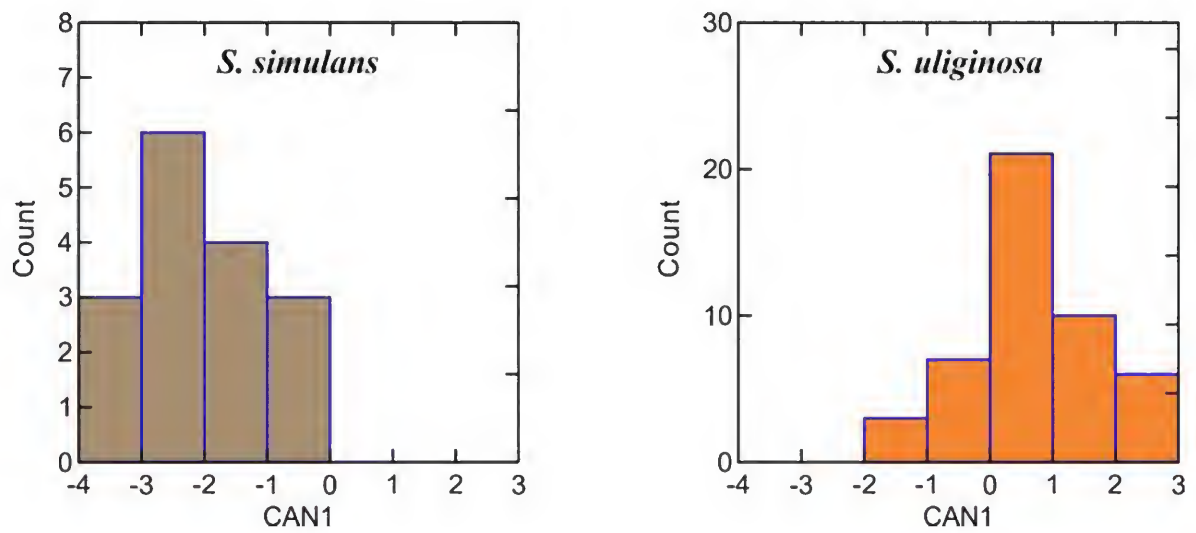

Figure 13. Histograms of canonical scores (CAN1) for *S. simulans* (left) and *S. uliginosa* s.l. (right).

Analysis 4: Two species level a priori groups analysis: Solidago simulans and S. ulginosa s.s.

In the STEPWISE discriminant analysis of 28 specimens of two species level a priori groups (*S. simulans* and *S. uliginosa* var. *uliginosa* only), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid series phyllary length (22.75),

number of ray florets (8.51), length of the longest lower inflorescence branches (5.14), and number of disc florets (4.54). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago simulans* and *S. uliginosa* had an F-to separate value of 12.477 (Wilks' lambda = 0.3155 df = 4 1 26; Approx. F= 12.4770 df = 4 23 prob = 0.0000).

In the Classificatory Discriminant Analysis of 28 specimens of the two species level a priori groups (*S. simulans* and *S. uliginosa* s.s.), percents of correct a posterori assignment to the same a priori group were 93% and 100%. The Classification matrix and Jackknife classification matrix are presented in Table 8. All of 13 specimens of the *S. uliginosa* s.s. a priori group (100%) were assigned a posteriori into the *S. uliginosa* s.s. group; 8 specimens with 97-100% probability, 4 specimens with 80-89% probability, and 1 specimen with 78% probability. Fourteen of the 15 specimens of the *S. simulans* a priori group (93%) were assigned a posteriori into the *S. simulans* group; 11 specimens with 92-100% probability, 2 specimens with 84-85% probability, and 1 specimen with 75% probability). One specimen of the *S. simulans* a priori groups were assigned to *S. uliginosa* s.s. with 53% probability (*Chapman s.n.* NY from middle Florida; a problematic specimen of uncertain identity and provenance).

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	***simulans***	***uliginosa s.s.***	**% correct**
simulans	14	1	93
uliginosa s.s.	0	13	100
Totals	14	14	96

Jackknifed classification matrix

Group	***simulans***	***uliginosa s.s.***	**% correct**
simulans	14	1	93
uliginosa s.s.	1	12	92
Totals	15	13	93

Histograms of canonical scores (CAN1) for *S. simulans* and *S. uliginosa* s.s. are shown in Fig. 14. The eigenvalue on the first axis was 2.170.

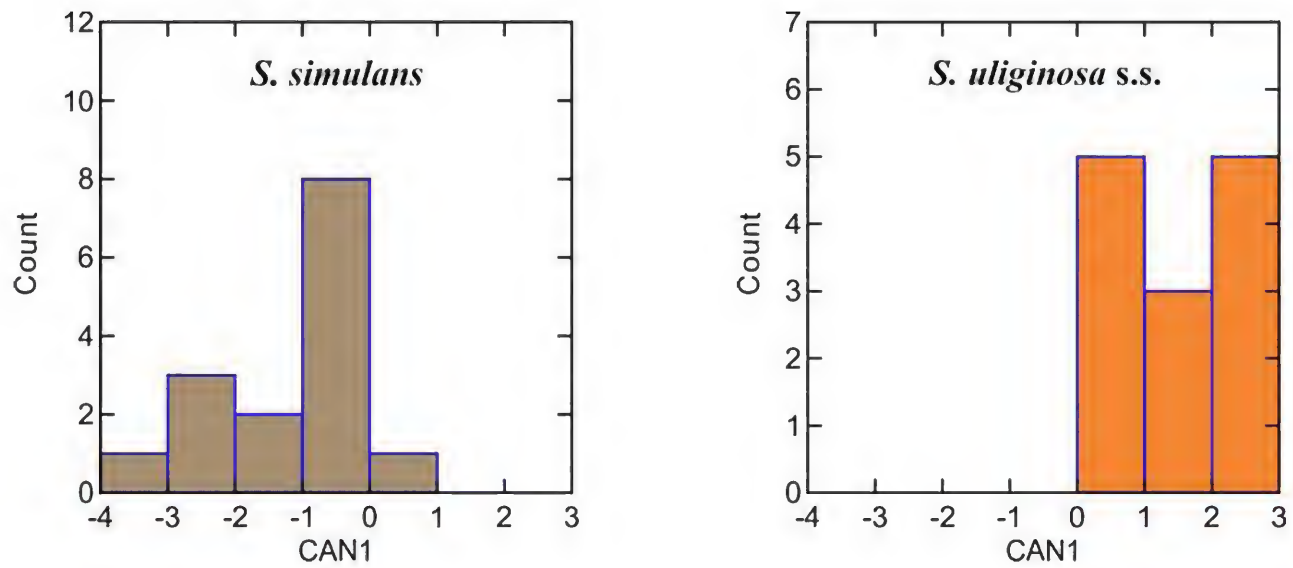

Figure 14. Histograms of canonical scores (CAN1) for *S. simulans* (left) and *S. uliginosa* (right).

Analysis 5: Four species level a priori groups analysis: Solidago uliginosa complex II

In the STEPWISE discriminant analysis of 105 specimens of four species level a priori groups *S. austrina*, *S. purshii* (combining predominantly diploid var. *peracuta* and *var. terrae-novae* of *S. uliginosa s.l.*), *S. simulans*, and *S. uliginosa* (including only tetraploid var. *uliginosa*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (29.35), number of nodes in the top 25% of stem below inflorescence (24.98), disc corolla lobe length (17.02), number of ray florets (16.91), mid series phyllary length, (7.44), and ray floret pappus length at anthesis (5.55). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 9. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. purshii* (52.645); the smallest separation was between *S. simulans* and *S. uliginosa* (5.131).

Table 9. Between groups F-matrix for the four species level a priori groups analysis (df = 6 93).

Group	*austrina*	*purshii*	*simulans*
purshii	59.038		
simulans	14.420	20.069	
uliginosa	17.399	10.455	5.131

Wilks' lambda = 0.0960 df = 6 3 98; Approx. F= 18.8498 df = 18 263 prob = 0.0000

In the Classificatory Discriminant Analysis of 105 specimens of the four species level a priori groups (*S. austrina*, *S. purshii*, *S. simulans* and *S. uliginosa* s.s.), percents of correct a posterori assignment to the same a priori group were 64% and 91%. The Classification matrix and Jackknife classification matrix are presented in Table 10. Thirty-one of the 34 specimens of the *S. purshii* a priori group (91%) were assigned a posteriori into the *S. purshii* group; 27 specimens with 92-100% probability, 2 specimens with 80-81% probability, 1 specimen with 73%, and 2 specimens with 68% (*Rouleau 5142* MT from Newfoundland; has a var. *terra-novae* inflorescence) and 65% probability (*Bouchard et al. 92408* MT from Newfoundland; has a var. *peracuta* inflorescence). Three specimens of the *S. purshii* a priori group were assigned to *S. uliginosa* with 82% (11% to *S. purshii*; *Semple & B. Semple 8714* WAT from the Manitoba-Ontario border), 66% probability (*Rouleau 5165* MT from Newfoundland), and 54% probability (*Semple & Keir 4711* WAT from New Brunswick; 102 cm tall diploid shoot with an elongated inflorescence with short ascending lower branches). Thirteen of 16 specimens of the *S. simulans* a priori group (87%) were assigned a posteriori into the *S. simulans* group; 2 specimens with 92% and 96% probabilities, 7 specimens with 81-89% probability, 3 specimens with 72-76% probability, and 1 specimen with 68% probability (*Totten s.n.* NCU from Macon Co., North Carolina; Fig. 7). Two specimens of the *S. simulans* a priori group were assigned to *S. uliginosa* with 58% probability (32% to *S. simulans*: *Semple 11590* WAT from Whiteside Mt., Jackson Co., North Carolina) and 49% probability (45% to *S. simulans*; *Krouse s.n.* NCU from Ashe Co., North Carolina). Thirty-three of 39 specimens of the *S. austrina* a priori group (85%) were assigned a posteriori into the *S. austrina* group; 28 specimens with 97-100% probability, 1 specimen with 86% probability, 2 specimens with 71-72% probability, 1 specimen with 62% probability (*Orzell & Bridges 17342* GA from Colquitt Co., Georgia), and 1 specimen with 59% probability (*Semple 11827* WAT from Walton Co., Georgia). Six specimens of the *S. austrina* a priori group were assigned to other species: 3 to *S. simulans* with 99% probability (*Lindholm s.n.* GA from Liberty Co., Florida), 98% probability (*Lazor 4587* MT from Liberty Co., Florida), and 67% probability (*Radford 19485* NCU from Montgomery Co., North Carolina); 2 specimens to *S. uliginosa* with 63% probability (*Semple et al.* 11857 WAT from Tennessee) and 60% probability

(*Beard 150* NCU from Lee Co., North Carolina; damaged inflorescence); and 1 specimen to *S. purshii* with 45% probability (*Heller 1284* NY from Rowan Co., North Carolina). Nine of the 14 specimens of the *S. uliginosa* s.s. a priori group (64%) were assigned a posteriori to *S. uliginosa*: 3 specimens with 92-100% probability, 3 specimens with 85-86% probability, 2 specimens with 76-77% probability, and 1 specimen with 60% probability (*Cusick 25744* NCU from West Virginia). Five specimens of the *S. uliginosa* s.s. a priori group were assigned a posteriori to other species: 2 specimens to *S. purshii* with 90% probability (*Gibson 1107* NCU from West Virginia) and 43% probability (*Downs 6769* NCU from West Virginia); and 3 specimens to *S. simulans* with 63% probability (*Chase 3386* USCH from Tazewell Co., Illinois), 59% probability (*Semple & Suripto* 9590 WAT from York Co., Maine; a robust shoot with a large inflorescence with long ascending spreading branches), and 53% probability (*Semple & Suripto 9524* WAT from New Jersey; a tetraploid, Fig. 2).

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four species level a priori groups; a posteriori placements to groups in rows.

Group	*austrina*	*purshii*	*simulans*	*uliginosa s.s*	% correct
austrina	33	1	3	2	85
purshii	0	31	0	3	91
simulans	0	0	13	2	87
uliginosa s.s.	0	2	3	9	64
Totals	33	34	19	16	84

Jackknifed classification matrix

Group	*austrina*	*purshii*	*simulans*	*uliginosa s.s*	% correct
austrina	33	1	4	2	82
purshii	0	31	0	3	91
simulans	0	0	13	2	87
uliginosa s.s	0	2	3	9	64
Totals	33	34	20	16	84

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 105 specimens of 4 species of *Solidago* subsect. *Maritimae* are presented in Fig. 15: groups (*S. austrina*, *S. purshii*, *S. simulans* and *S. uliginosa* s.s.). Eigenvalues on the three axes were 3.873, 0.718, and 0.0.224.

Analysis 6: Four species level a priori groups analysis: Solidago uliginosa complex III

In the STEPWISE discriminant analysis of 102 specimens of four species level a priori groups (*S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* (including *S. purshii*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (28.27), number of ray florets (14.56), number of nodes in the top 25% of stem below inflorescence (14.20), mid series phyllary length (6.38), mid stem leaf length (6.06), and ray floret lamina length (5.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of $p = 0.0000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 11. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. uliginosa* (47.624); the smallest separation was between *S. terrae-novae* and *S. uliginosa* (2.849).

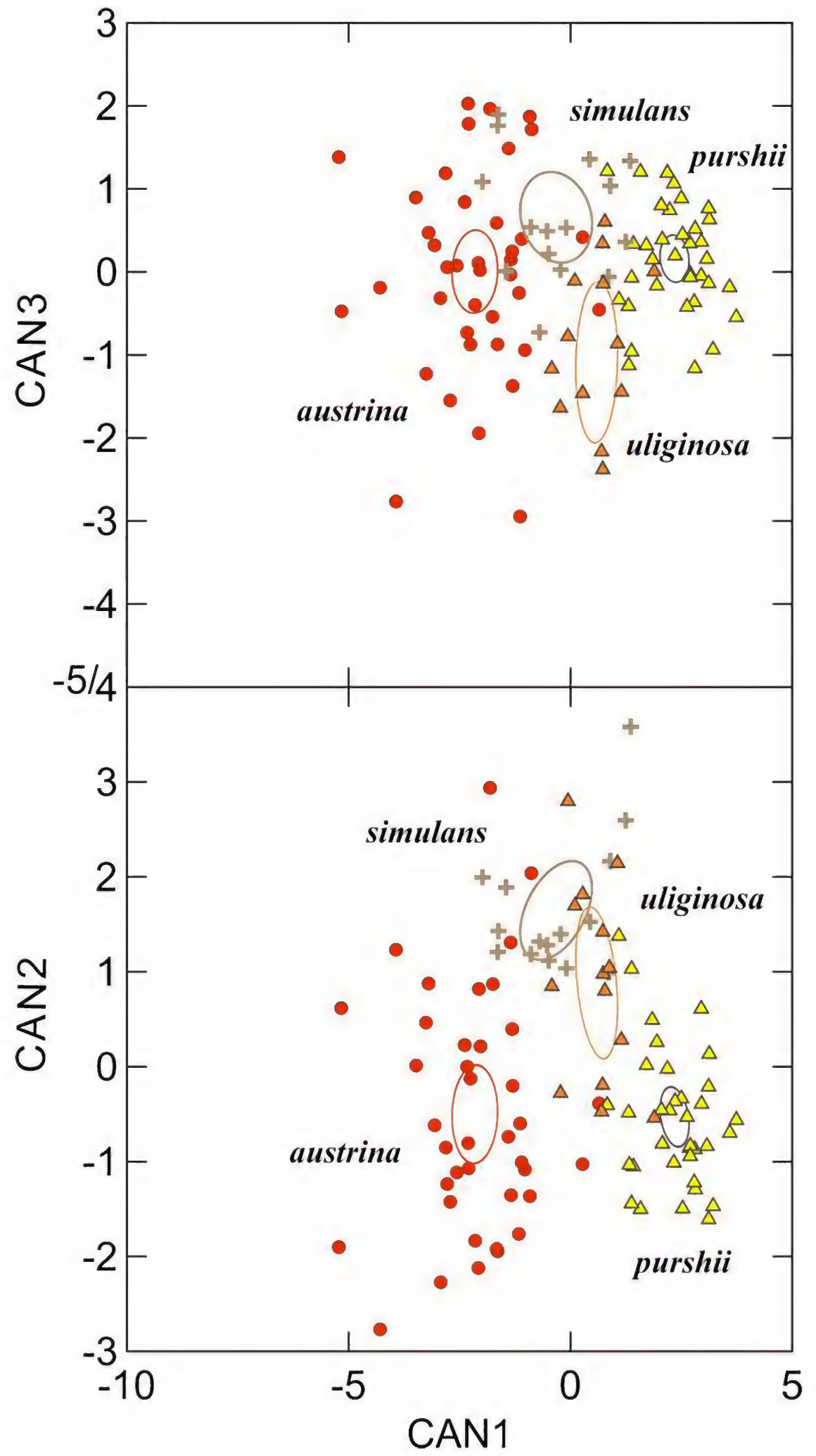

Figure 15. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 105 specimens of 4 a priori groups of the *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. purshii* (yellow triangles), *S. simulans* (brown +s), *S. uliginosa* (orange triangles).

In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups (*S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* including *S. purshii*), percents of correct a posteriori assignment to the same a priori group ranged from 68-87%. The Classification matrix and Jackknife classification matrix are presented in Table 12. Thirty-four of the 39 specimens In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups

Table 11. Between groups F-matrix for the four species level a priori groups analysis (df = 6 93).

Group	*austrina*	*simulans*	*terrae-novae*
simulans	19.115		
terrae-novae	19.985	7.003	
uliginosa	47.624	9.449	2.849

Wilks' lambda = 0.1281 df = 6 3 98; Approx. F= 15.6023 df = 18 263 prob = 0.0000

(*S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* including *S. purshii*), percents of correct a posteriori assignment to the same a priori group ranged from 68-87%. The Classification matrix and Jackknife classification matrix are presented in Table 12. Thirty-four of the 39 specimens of the *S. austrina* a priori group (87%) plus 1 specimen only included a posteriori were assigned a posteriori into the *S. austrina* group; 31 specimens with 91-100% probability, 1 specimen with 88% probability, 1 specimen with 67% probability, and 2 specimens with 55% probability (*Heller 1284* NY from Rowan Co., North Carolina) and 54% probability (*Semple & Suripto 9786* WAT a diploid from Clarendon Co., South Carolina). Four specimens of the *S. austrina* a priori groups were assigned to other species: 3 specimens to *S. simulans* with 89% (*Lindholm s.n.* GA from Liberty Co., Florida), 81% probability (*Lazor 4587* MT from Liberty Co., Florida), and 77% probability (*Radford 19485* NCU from Montgomery Co., North Carolina); and 1 specimen to *S terrae-novae* with 90% probability (*Beard 150* NCU from Lee Co., North Carolina; damaged inflorescence). Thirteen of 16 specimens of the *S. simulans* a priori group (81%) were assigned a posteriori into the *S. simulans* group; 7 specimens with 90-100% probability, 2 specimens with 85% and 81% probabilities, and 3 specimens with 75-79%. Three specimens of the *S. simulans* a priori group were assigned to other species: 2 specimens to *S. terrae-novae* with 62% probability (*Chapman s.n.* NY from middle Florida; a problematic specimen of uncertain identity and provenance) and 46% probability (*Godfrey 6949* GH from Scotland Co., North Carolina); and 1 specimen to *S. uliginosa* with 49% probability (*Semple 11590* WAT from Whiteside Mt., Jackson Co., North Carolina). Seven of the ten specimens of the *S. terrae-novae* a priori groups (70%) plus 1 specimen only included a posteriori were assigned to the *S. terrae-novae* group: 2 specimens with 96% probability, 2 specimens with 88% and 81% probability, 1 specimen with 78% probability, 1 specimen with 67% probability, and 2 specimens with 53% probability (*Rouleau 5302* MT from SW Newfoundland) and 52% probability (*Rouleau 7382* MT from SW Newfoundland; robust shoot with broad corymboid secund conical inflorescence). Three specimens of the *S. terrae-novae* a priori group were assigned a posteriori to *S. uliginosa* with 67% probability (*Rouleau 5165* MT from Newfoundland; the second sheet of this number), 61% probability (*Rouleau 5307* MT from SW Newfoundland; small and robust shoots with small corymboid inflorescences or a larger broad inflorescence with branches with small corymbiform arrangements of heads), and 40% probability (*Rouleau 5165* MT from Newfoundland, Fig. 4). Twenty-five of the 37 specimens of the enlarged *S. uliginosa* a priori group (68%) were assigned a posteriori to the *S. uliginosa* group: 6 specimens with 91-98% probability, 3 specimens with 80-84% probability, 6 specimens with 70-79% proability, 4 specimens with 60-65% probability, 1 specimen with 47% probability (*Rouleau 8411* MT from eastern Newfoundland), and 1 specimen with 39% probability (*Downs 6769* NCU from West Virginia; the inflorescence has spreading arching lower branches typical for var. *uliginosa*). Twelve specimens of the enlarged *S. uliginosa* a priori group were assigned to other species: 6 specimens to *S. simulans* with 77% probability (*Semple & Suripto 9524* WAT from New Jersey; a tetraploid, Fig. 2), 60% probability (*Chase 3386* USCH from Tazewell Co., Illinois), 57% probability (*Cusick 25744* NCU from West Virginia), 57% probability (*Bouchard et al. 92408* MT from Newfoundland; small shoot with a var. *peracuta*-like inflorescence), 48% probability (*Semple & Suripto* 9590 WAT from York Co., Maine; a robust shoot with a large

inflorescence with long ascending spreading branches), and 42% (*Semple 11814* WAT from New Jersey); and 6 specimens to *S. terrae-novae* with 64% probability (*Rouleau 7022* MT from northcentral Newfoundland; a 74 cm tall shoot), 58% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4), 57% probability (*Semple & Keir 48*97 WAT from New Brunswick; the inflorescence has long ascending diverging branches), 51% probability (*Semple & Suripto 9576* WAT, tetraploid from Massachusetts).

Table 12. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four species level a priori groups; a posteriori placements to groups in rows.

Group	*austrina*	*simulans*	*terrae-novae*	*uliginosa*	% correct
austrina	34	3	2	0	87
simulans	0	13	2	1	81
terrae-novae	0	0	7	2	70
uliginosa	0	6	6	25	68
Totals	34	22	17	29	77

Jackknifed classification matrix

Group	*austrina*	*simulans*	*terrae-novae*	*uliginosa*	% correct
austrina	33	4	2	0	85
purshii	1	12	2	1	75
terrae-novae	0	0	7	3	70
uliginosa	0	6	6	25	68
Totals	34	22	17	29	75

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 105 specimens of 4 species of *Solidago* subsect. *Maritimae* are presented in Fig. 16: *S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* (including *S. purshii*). Eigenvalues on the three axes were 3.408, 0.508, and 0.174.

Analysis 7: Five species level a priori groups analysis: Solidago uliginosa complex III

In the STEPWISE discriminant analysis of 102 specimens of five species level a priori groups (*S. austrina*, *S. purshii, S. simulans*, *S. terrae-novae*, and and expanded *S. uliginosa* (including *S. purshii*), the following seven traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (21.45), number of ray florets (12.82), number of nodes in the top 25% of stem below inflorescence (10.03), disc corolla lobe length (7.20), mid stem leaf length (6.01), mid series phyllary length (4.78), and ray floret lamina length (4.22). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.0000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 13. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. purshii* (46.301); the smallest separations were between *S. purshii* and *S. terrae-novae* (2.722), *S. terrae-novae* and *S. uliginosa* (3.449), and *S. simulans* and *S. uliginosa* (4.686), and *S. purshii* and *S. uliginosa* (5.456).

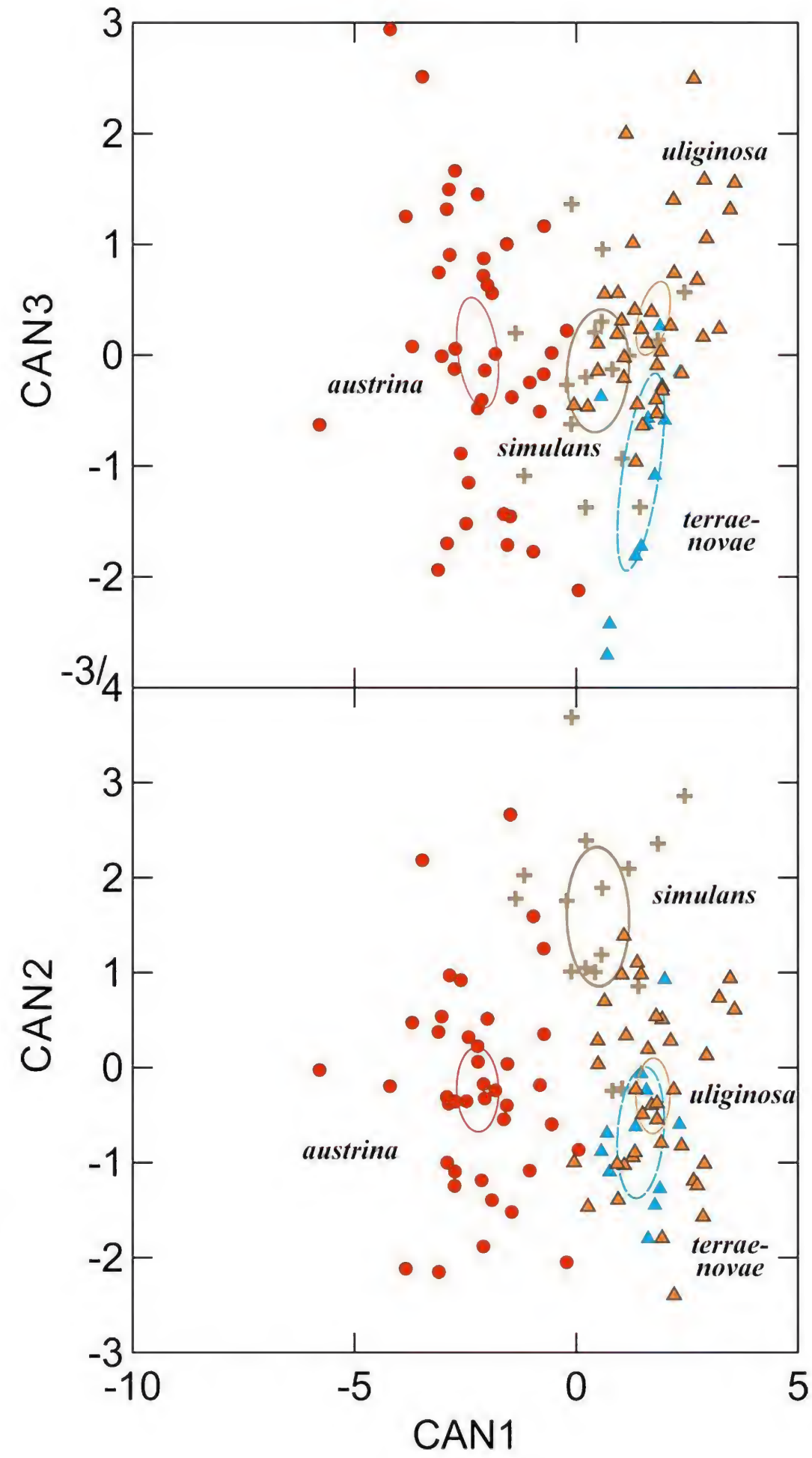

Figure 16. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 104 specimens in 4 a priori groups of the *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. simulans* (brown +s), *S. terrae-novae* (including; light blue triangles), and an expanded *S. uliginosa* (including *S. purshii*; orange triangles).

Table 13. Between groups F-matrix for the four species level a priori groups analysis (df = 7 91).

Group	*austrina*	*purshii*	*simulans*	*terrae-novae*
purshii	46.301			
simulans	17.101	10.976		
terrae-novae	20.747	2.722	7.043	
uliginosa	17.303	5.456	4.686	3.449

Wilks' lambda = 0.0840 df = 7 4 97; Approx. F= 11.6046 df = 28 329 prob = 0.0000

In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups (*S. austrina*, *S. purshii*, *S. simulans S. terrae-novae*, and *S. uliginosa* including *S. purshii*) plus 1 specimen each of *S. austrina* and *S. terrae-novae* only included a posteriori, percents of correct a posterori assignment to the same a priori group were 60-88%. The Classification matrix and Jackknife classification matrix are presented in Table 14. Fourteen of the 16 specimens of the *S. simulans* a priori group (88%) were assigned a posteriori into the *S. simulans* group; 5 specimens with 91-94% probability, 2 specimens with 89% and 84% probability, 4 specimens with 71-79% probability, 2 specimens with 64% probability (*Krouse s.n.* NCU from Ashe Co., North Carolina) and 63% probability (*Godfrey 50724* GH from Moore Co., North Carolina), and 1 specimen with 55% probability (*Godfrey 6949* GH from Scotland Co., North Carolina). Two specimens of the *S. simulans* a priori groups were assigned to *S. uliginosa* with 73% probability (*Chapman s.n.* NY from middle Florida; a problematic specimen of uncertain identity and provenance) and 40% probability (*Semple 11590* WAT from Whiteside Mt., Jackson Co., North Carolina). Thirty-four of the 39 specimens of the *S. austrina* a priori group (87%) plus 1 additional specimen only included a posteriori were assigned a posteriori into the *S. austrina* group; 31 specimens with 96-100% probability, 1 specimen with 88% probability, 1 specimen with 63% probability (*Sorrie 7711* NCU from Moore Co., North Carolina), and 1 specimen with 39% probability (*Heller 1284* NY from Rowan Co., North Carolina). Five specimens of the *S. austrina* a priori group were assigned to other species; 3 specimens to *S. simulans* with 86% probability (*Lindholm s.n.* GA from Liberty Co., Florida), 83% probability (*Lazor 4587* MT from Liberty Co., Florida), and 64% probability (*Radford 19485* NCU from Montgomery Co., North Carolina); 1 specimen to *S. terrae-novae* with 61% probability (*Beard 150* NCU from Lee Co., North Carolina; damaged inflorescence); and 1 specimen to *S. uliginosa* with 53% probability (*Semple et al.* 11857 WAT from Tennessee). Seventeen of 24 specimens of the *S. purshii* a priori group (71%) were assigned a posteriori to *S. purshii*; 6 specimens with 97-99% probability, 2 specimens with 88% and 84% probabilities, 1 specimen with 72% probability, 3 specimens with 58% probability (*Shchepanek & White 2851* MT from Newfoundland), 54% probability (*Semple & Brammall 2827* WAT from Cochrane Dist., Ontario; robust diploid), and 51% probability (*Bouchard et al. 92408* MT from Newfoundland), and 2 specimens with 48% probability (*Semple & Keir 48*97 WAT from New Brunswick; robust diploid) and 44% probability (*Ownbey & Hsi 4214* NCU from Minnesota). Six specimens of the *S. purshii* a priori group were assigned to other species: 4 to *S. terrae-novae* with 63% probability (*Rouleau 7022* MT from northcentral Newfoundland), 60% probability (*Torrey s.n.* NY from New York), 55% probability (*Semple & Keir 48*97 WAT from New Brunswick, second shoot on sheet), and 50% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4); 1 to *S. simulans* with 68% probability (*Chase 3386* USCH from Illinois); and 1 to *S. uliginosa* with 61% probability (*Semple & Keir 4711* WAT from New Brunswick; 102 cm tall diploid shoot with an elongated inflorescence with short ascending lower branches). Eight of 13 specimens of the *S. uliginosa* a priori group (62%) were assigned a posteriori to *S. uliginosa*; 3 specimens with 94-99% probability, 1 specimen with 88% probability, 1 specimen with 79% probability, 2 specimens with 67% probability and 60% probability (*Semple 11814* WAT from New Jersey; tetraploid), and 1 specimen with 33% probability (32% to *S. terrae-novae*, 19% to *S. austrina, and 16% to S. simulans*; *Downs 6769* NCU from West Virginia). Four specimens of the *S. uliginosa* a priori group were assigned to other species: 1 to *S. purshii* with 76% probability (*Morton & Venn NA14272* TRT from Nipigon, Ontario; diploid with long diverging inflorescence branches); 3 specimens to *S. simulans* with 65% probability (*Semple & Suripto 9524* WAT from New Jersey; a tetraploid, Fig. 2), 54% probability (*Semple & Suripto* 9590 WAT from York Co., Maine), and 51% probability (*Cusick 25744* NCU from West Virginia); and 1 specimen to *S. terrae-novae* with 40% probability (38% to *S. purshii* and 21% to *S. uliginosa*; *Gibson 1107* NCU from West Virginia). Six of 10 specimens of the *S. terrae-novae* a priori group (60%) plus 1 additional specimen only included a posteriori were assigned a posteriori to *S. terrae-novae*; 2 specimens with 94% and 91% probabilities, 1 specimen with 89% probability, 2 specimens with 78% probability and 76% probability, 1 specimen with 68%% probability, and 1 specimens with 55%

probability (*Rouleau 5302* MT from SW Newfoundland). Four specimens of the *S. terrae-novae* a priori group were assigned to other species: 3 specimens to *S. purshii* with 69% probability (*Rouleau 5307* MT from SW Newfoundland), 69% probability (*Rouleau 5165* MT from Newfoundland), and 48% probability (*Rouleau 7382* MT from SW Newfoundland); and 1 specimen to *S. simulans* 44% probability (*Rouleau 5165* MT from Newfoundland, Fig. 4).

Table 14. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of five species level a priori groups; a posteriori placements to groups in rows.

Group	*austrina*	*S. purshii*	*simulans*	*terrae-novae*	*uliginosa*	% correct
austrina	34	0	3	1	1	87
purshii	0	17	1	4	2	71
simulans	0	0	14	0	2	88
terrae-novae	0	3	1	6	0	60
uliginosa	0	1	3	1	8	62
Totals	34	21	22	12	13	77

Jackknifed classification matrix

Group	*austrina*	*S. purshii*	*simulans*	*terrae-novae*	*uliginosa*	% correct
austrina	32	0	3	1	3	82
purshii	0	16	1	5	2	67
simulans	1	0	13	0	2	81
terrae-novae	00	3	1	6	0	60
uliginosa	0	1	3	2	7	54
Totals	33	20	21	14	14	73

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 104 specimens of 5 species level groups (*S. austrina*, *S. purshii*, S. *simulans*, *S. terrae-novae*, and *S. uliginosa*) of *Solidago* subsect. *Maritimae* are presented in Fig. 17. Eigenvalues on the four axes were 4.234, 0.552, 0.243, and 0.179.

Analysis 8: Three varietal level a priori groups analysis of Solidago uliginosa

In the STEPWISE discriminant analysis of 47 specimens of three varietal level a priori groups in *S. uliginosa* (var. *peracuta*, var. *terrae-novae*, and var. *uliginosa*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret corolla lobe length (10.41), ray floret pappus length at anthesis (7.95), and number of nodes in the top 25% of the stem below the inflorescence (6.21). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 15. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. *terrae-novae* and var. *uliginosa* (14.538); the smallest separation was between var. *peracuta* and var. *terrae-novae* (5.425).

Table 15. Between groups F-matrix for the three varietal level a priori groups analysis (df = 3 42).

Group	*peracuta*	*terrae-novae*
terrae-novae	5.425	
uliginosa	14.538	12.875

Wilks' lambda = 0.3341 df = 3 2 44; Approx. F= 14.538 df = 6 84 prob = 0.0000

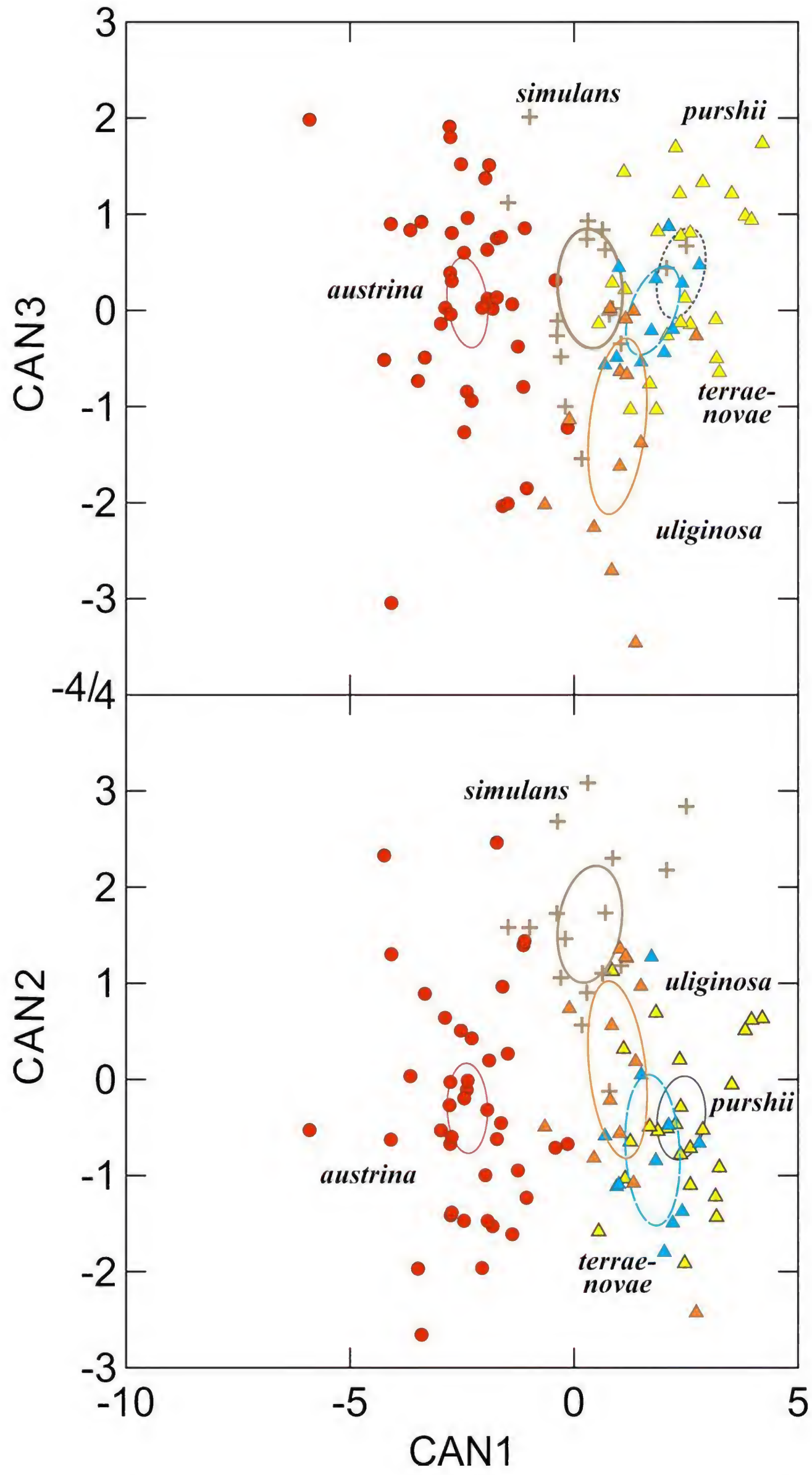

Figure 17. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 104 specimens in 5 a priori groups of the *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. purshii* (yellow triangles), *S. simulans* (brown +s), *S. terrae-novae* (including; light blue triangles), and *S. uliginosa* s.s. (orange triangles).

In the Classificatory Discriminant Analysis of 47 specimens of the three varietal level a priori groups in *S. uliginosa* (var. *peracuta*, var. *terrae-novae*, and var. *uliginosa*) plus 1 additional specimen included a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 67-90%. The Classification matrix and Jackknife classification matrix are presented in Table 16. Nine of the 10 specimens of the var. *terrae-novae* a priori group (90%) plus 1 specimen included a posteriori were assigned a posteriori into the var. *terrae-novae* group; 2 specimens with 90% and 93% probability, 2 specimens with 85-86% probability, 1 specimen with 74% probability, 3 specimens with 61-66% probability, and 2 specimens with 49% probability (*Rouleau 5302* MT from SW Newfoundland; small shoots with broad compact inflorescences) and 48% probability (*Rouleau 5165* MT from Newfoundland, Fig. 4). One specimen of the var. *terrae-novae* a priori group was assigned a posteriori to var. *peracuta* (37% to var. *terrae-novae* and 9% to var. *uliginosa*; *Rouleau 5142* MT). Ten of 13 specimens of the var. *uliginosa* a priori group (77%) were assigned to that group: 6 specimens with 97-100% probability, 2 specimens with 73% and 75% probabilities, and 2 specimens with 64% and 62% probabilities. Three specimens of the var. *uliginosa* a priori group were assigned a posteriori to other varieties: 2 specimens to var. *peracuta* with 58% probability (*Morton & Venn NA14272* TRT from Nipigon, Ontario; the inflorescence is rather broad for var. *peracuta*) and 41% probability (*Downs 6769* NCU from West Virginia; the inflorescence has spreading arching lower branches typical for var. *uliginosa*) and 1 specimen to var. *terrae-novae* with 55% probability (*Gibson 1107* NCU from West Virginia; the inflorescence is elongated and narrow). Sixteen of 24 specimens of the var. *peracuta* a priori group (67%) were assigned a posteriori to var. *peracuta*: 2 specimens with 97% and 95% probabilities, 5 specimens with 80-89% probability, 6 specimens with 72-79% probability, 2 specimens with 65-66% probability, and 1 specimen with 53% probability (45% to var. *terrae-novae*; *Rousseau 51455* MT from L'Île-d'Anticosti, Québec; the shoot scored had a more compact inflorescence, while two other shoots not scored had larger more open inflorescences with spreading, arching lower branches more typical of var. *terrae-novae*). Seven specimens of the var. *peracuta* a priori group were assigned a posteriori to other varieties: 4 specimens to var. *terrae-novae* with 84% probability (*Semple & Keir 48*97 WAT from New Brunswick; the inflorescence has long ascending diverging branches; the other shoot on the sheet was also scored and assigned a posteriori to var. *peracuta* with 80% probability), 82% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4), 61% probability (*Semple 9072* WAT from Wisconsin; a robust diploid plant with an elongated inflorescence with short spreading arching branches), and 50% probability (48% to var. *peracuta*; *Rouleau 7022* MT from northcentral Newfoundland; a 74 cm tall shoot with a large inflorescence with ascending branches typical of var. *peracuta*); 3 specimens were assigned a posteriori to var. *uliginosa* with 95% probability (*Chase 3386* USCH from Illinois that should have been assigned var. *uliginosa* due to its long spreading inflorescence branches and geographic location), 61% probability (*Semple & B. Semple 8714* WAT from near the Ontario-Manitoba border; a robust shoot with elongated inflorescence with ascending branches) and 53% probability (*Ownbey & Hsi 4214* NCU from Minnesota; a mid size shoot with inflorescence with long diverging lower branches more typical of var. *uliginosa*).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 48 specimens of var. *peracuta*, var. *terrae-novae*, and var. *ulginosa* of *Solidago uliginosa* is presented in Fig. 18. Eigenvalues on the first two axes were 1.166 and 0.381.

Analysis 9: Alternative Analysis of four a priori groups: S. austrina, S. purshii, S. terrae-novae and S. uliginosa (including S. simulans)

In the STEPWISE discriminant analysis of 104 specimens of four species level a priori groups (*S. austrina*, *S. purshii*, *S. terrae-novae*, and *S. uliginosa* including *S. simulans*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (24.82), number of nodes in the top 25% of stem below inflorescence (13.56), number of ray florets (12.67), disc corolla lobe length (11.55), mid stem leaf length (7.70), and ray

Table 16. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three variety level a priori groups in *Solidago uliginosa*; a posteriori placements to groups in rows.

Group	*purshii*	*terrae-novae*	*uliginosa*	% correct
purshii	16	4	4	67
terrae-novae	1	9	0	90
uliginosa	2	1	10	77
Totals	16	14	14	74

Jackknifed classification matrix

Group	*purshii*	*terrae-novae*	*uliginosa*	% correct
purshii	16	4	4	67
terrae-novae	1	8	1	80
uliginosa	2	2	9	69
Totals	16	14	14	70

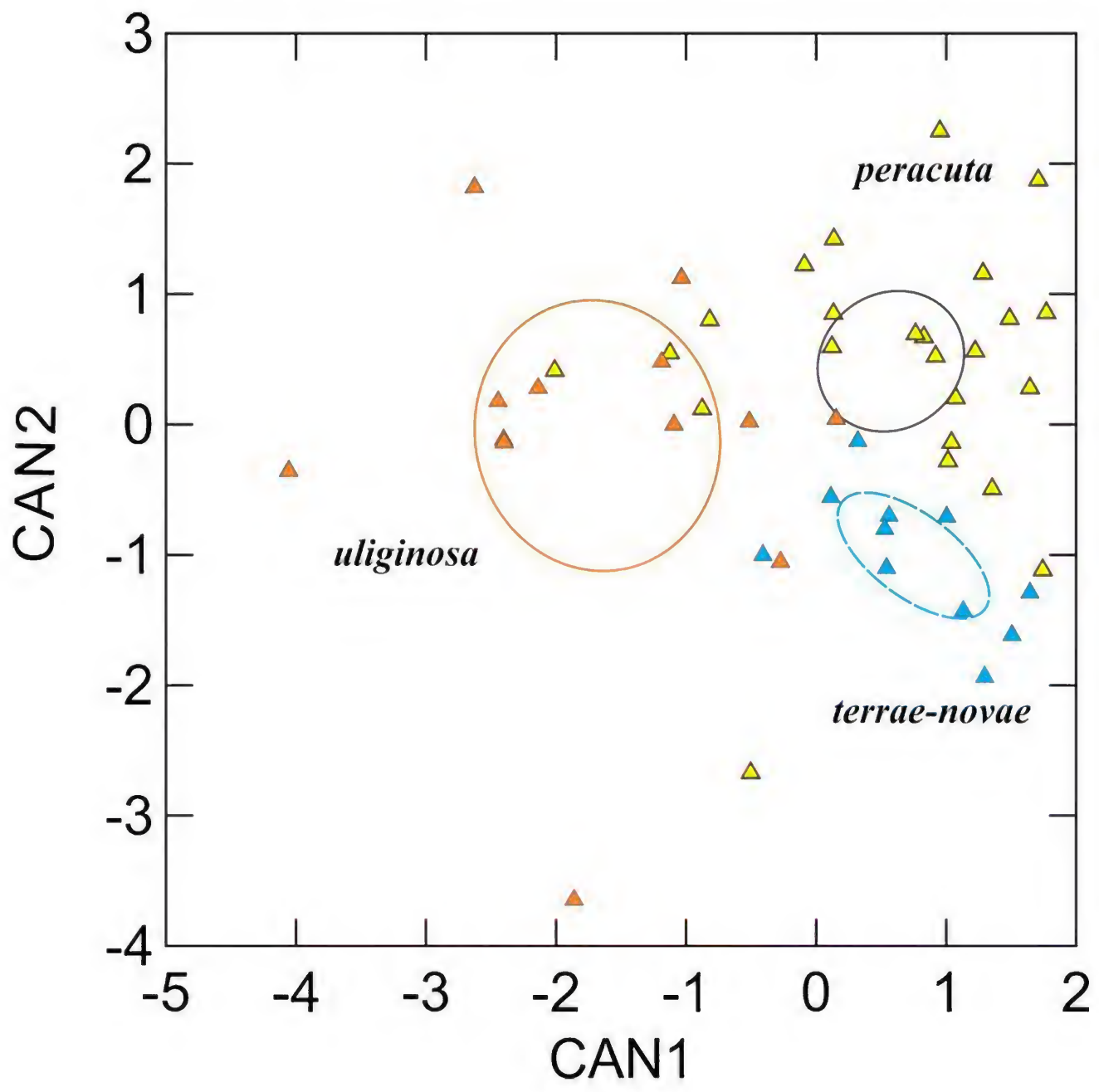

Figure 18. Plot of canonical scores (CAN1 vs. CAN2) for 48 specimens of *S. uliginosa*: var. *peracuta* (yellow triangles), var. *terrae-novae* (light blue triangles), and var. *uliginosa* (orange triangles).

floret lamina length (6.07). Lower inflorescence branch length was not selected as strongly discriminating (0.40). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.0000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 17. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was

between *S. austrina* and *S. purshii* (53.771); the smallest separations were between *S. purshii* and *S. terrae-novae* (3.190) and *S. terrae-novae* and *S. uliginosa* s.s. (6.396)

Table 17. Between groups F-matrix for the four species level a priori groups analysis (df = 6 93).

Group	*austrina*	*purshii*	*terrae-novae*
purshii	53.771		
terrae-novae	24.771	3.190	
uliginosa	26.825	12.538	6.396

Wilks' lambda = 0.1778 df = 6 3 98; Approx. F= 16.5093 df = 18 263 prob = 0.0000

In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups (*S. austrina*, *S. simulans S. terrae-novae*, and *S. uliginosa* including *S. purshii*) plus 1 each of specimens of *S. austrina* and *S. terrae-novae* only included a posteriori, percents of correct a posterori assignment to the same a priori group were 70% and 92%. The Classification matrix and Jackknife classification matrix are presented in Table 18. Thirty-six of the 39 specimens of the *S. austrina* a priori group (92%) plus 1 specimen only included a posteriori were assigned a posteriori into the *S. austrina* group; 31 specimens with 94-100% probability, 2 specimens with 85% and 88% probabilities, 1 specimens with 99% probability, and 3 specimens with 57% (*Heller 1284* NY from Rowan Co., North Carolina), 56% probability (*Semple & Suripto 9786* WAT a diploid from Clarendon Co., South Carolina), and 54% probability (*Radford 19485* NCU from Montgomery Co., North Carolina). Three specimens of the *S. austrina* a priori groups were assigned to other species: 2 specimens to *S. uliginosa* with 87% (*Semple et al.* 11857 WAT from Tennessee) and 54% probability (*Sorrie 7711* NCU from Moore Co., North Carolina); and 1 specimen to *S. terrae-novae* with 63% probability (*Beard 150* NCU from Lee Co., North Carolina; damaged inflorescence). Eighteen of 23 specimens of the *S. purshii* a priori group (78%) were assigned a posteriori into the *S. purshii* group; 7 specimens with 91-99% probability, 1 specimen with 87% probability, 3 specimens with 72-75% probability, 3 specimens with 61-62% probability, 3 specimens with 58% probability (*Shchepanek & White 2851* MT from Newfoundland), 56% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4), and 54% probability (*Semple & Keir 48*97 WAT from New Brunswick; shoot on right side of sheet), and 1 specimen with 44% probability (*Ownbey & Hsi 4214* NCU from Minnesota; a mid size shoot with inflorescence with long diverging lower branches more typical of var. *uliginosa*). Five specimens of the *S. purshii* a priori group were assigned to other species: 3 specimens to *S. terrae-novae* with 68% probability (*Torrey s.n.* NY from New York; the elongate inflorescence has long ascending lower branches), 66% probability (*Semple & Keir 48*97 WAT from New Brunswick; shoot on left side of sheet), and 66% probability (*Rouleau 7022* MT from northcentral Newfoundland; a 74 cm tall shoot with a large inflorescence with ascending branches); and 2 specimens to *S. uliginosa* with 66% probability (*Semple & B. Semple 8714* WAT from near the Ontario-Manitoba border; a robust shoot with elongated inflorescence with ascending branches) and 47% probability (*Semple & Keir 4711* WAT from New Brunswick; 102 cm tall diploid shoot with an elongated inflorescence with short ascending lower branches). Seven of 10 specimens of the *S. terrae-novae* a priori group (70%) plus 1 specimen only included a posteriori were assigned a posteriori into the *S. terrae-novae* group; 3 specimens with 90-96% probability, 1 specimen with 81% probability, 1 specimen with 79% probability, 1 specimen with 68% probability, and 2 specimens with 57% probability (*Rouleau 5302* MT from SW Newfoundland; small shoots with broad compact inflorescences) and 51% probability (*Rouleau 7382* MT from SW Newfoundland; robust shoot with broad corymboid secund conical inflorescence). Five specimens of the *S. terrae-novae* a priori group

were assigned to other species: 2 specimens to *S. purshii* with 73% probability (*Rouleau 5165* MT from SE Newfoundland, second sheet of this collection) and 72% probability (*Rouleau 5307* MT from SW Newfoundland; small and robust shoots with small corymboid inflorescences or a larger broad inflorescence with branches with small corymbiform arrangements of heads); and 1 specimen to *S. uliginosa* with 71% probability (*Rouleau 5165* MT from SE Newfoundland, Fig. 4).

Table 18. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four species level a priori groups; a posteriori placements to groups in rows.

Group	*austrina*	*purshii*	*terrae-novae*	*uliginosa*	% correct
austrina	36	0	1	2	92
purshii	0	18	3	2	78
terrae-novae	0	2	7	2	70
uliginosa	2	1	1	26	87
Totals	38	21	12	31	85

Jackknifed classification matrix

Group	*austrina*	*purshii*	*terrae-novae*	*uliginosa*	% correct
austrina	34	0	1	4	87
purshii	0	18	3	2	78
terrae-novae	0	3	6	1	60
uliginosa	2	1	1	26	87
Totals	34	21	11	33	82

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 104 specimens of 4 species groups are presented in Fig. 19: groups (*S. austrina*, *S. purshii*, *S. terrae-novae*, and *S. uliginosa* including *S. simulans*). Eigenvalues on the first three axes were 4.084, 0.415, and 0.180.

Analysis 10: Analysis of S. terrae-novae and S. uliginosa (including S. purshii)

In the STEPWISE discriminant analysis of 47 specimens of two species level a priori groups (*S. terrae-novae* and *S. uliginosa* including *S. purshii*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (35.24), number of ray florets (14.28), and ray floret pappus length (7.93). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago terrae-novae* and *S. uliginosa* had an F-to separate value of 18.363 (Wilks' lambda = 0.4384 df = 3 1 45; Approx. F= 18.3633 df = 3 43 prob = 0.0000).

In the Classificatory Discriminant Analysis of 47 specimens of the two species level a priori groups (S. *terrae-novae* and *S. uliginosa* including *S. purshii*) plus 1 specimen each of of *S. terrae-novae* and *S. uliginosa* only included a posteriori, percents of correct a posterori assignment to the same a priori group were 100% and 92%. The Classification matrix and Jackknife classification matrix are presented in Table 19. Ten of the 10 specimens of the *S. terrae-novae* a priori group (100%) plus 1 additional specimen only included a posteriori were assigned to the *S. terrae-novae* group: 8 with 92-100% probability, 2 with 89% and 85% probabilities, and 1 with 63% probability (*Rouleau 5165* MT from SE Newfoundland, second sheet of this collection). Thirty-three of the 36 specimens of the *S. uliginosa* a priori group (92%) plus 1 specimen only included a posteriori were

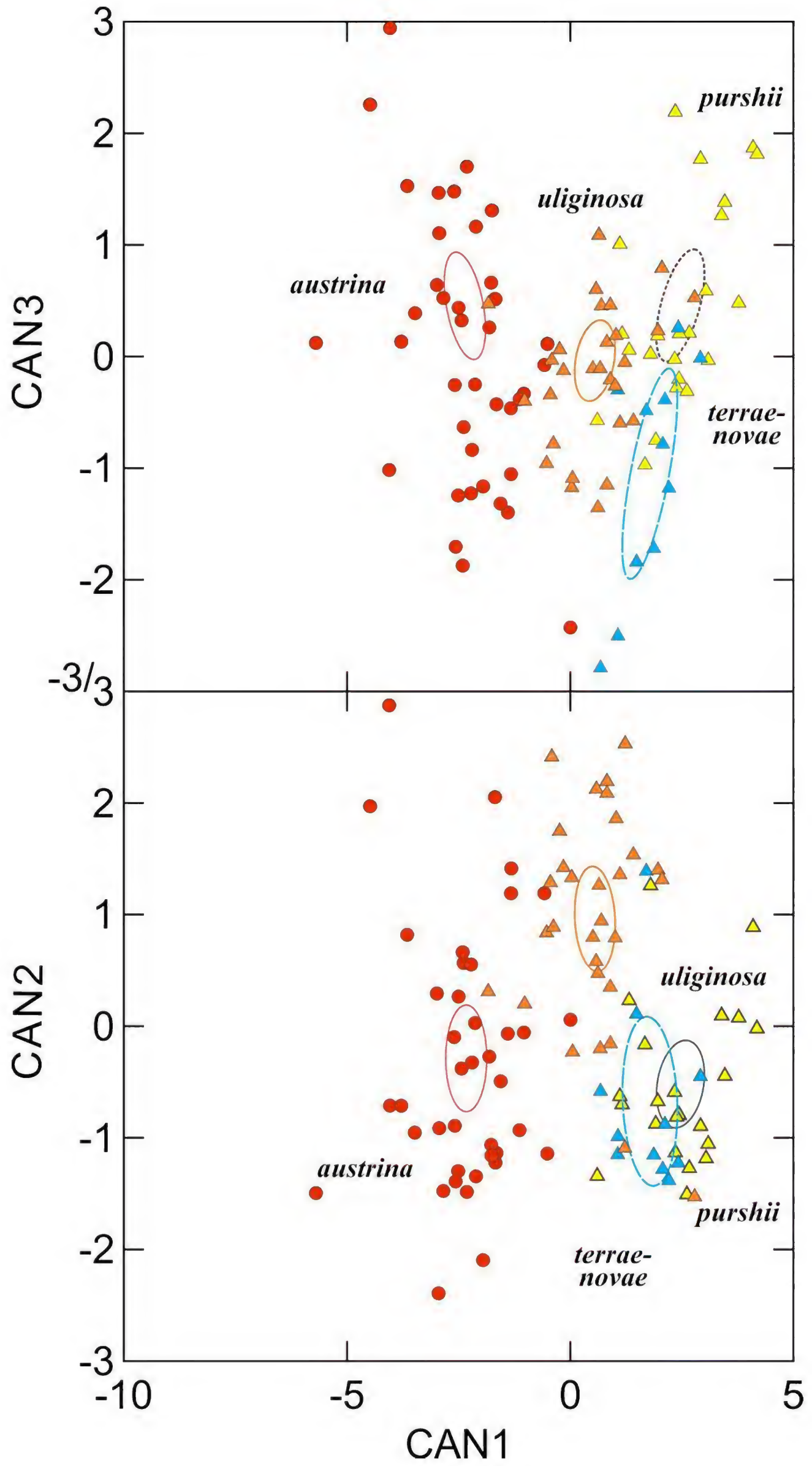

Figure 19. Plot of canonical scores (CAN1 vs. CAN2) for 104 specimens of *S. austrina* (red dots), *S. uliginosa*: var. *peracuta* (yellow triangles), var. *terrae-novae* (light blue triangles), and var. *uliginosa* including *S. simulans* (orange triangles).

into the *S. uliginosa* group; 27 specimens with 93-100% probability, 4 specimens with 86-88% probability, 1 specimen with 62% probability, and 2 specimens with 58% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4) and 52% probability (*Semple & Suripto 9576* WAT a tetraploid from Massachusetts; short divergent lower inflorescence branches). Three specimens of the *S. uliginosa* a priori group were assigned to *S. terrae-novae* with 94% (*Semple & Keir 48*97 WAT from New Brunswick; the inflorescence has long ascending diverging branches), 54% probability (*Semple & Suripto* 9590 WAT from York Co., Maine; a robust shoot with a large inflorescence with long ascending spreading branches), and 52% probability (*Semple 9072* WAT from Wisconsin; a robust diploid plant with an elongated inflorescence with short spreading arching branches).

Histograms of canonical scores (CAN1) for 49 individuals of *S. terrae-novae* and *S. uliginosa* (including *S. purshii*) are shown in Fig. 20. The eigenvalue on the first axis was 1.281.

Table 19. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	***terrae-novae***	***uliginosa***	**% correct**
terrae-novae	11	0	100
uliginosa	3	34	92
Totals	14	34	96

Jackknifed classification matrix

Group	***terrae-novae***	***uliginosa***	**% correct**
terrae-novae	11	0	100
uliginosa	4	33	89
Totals	15	33	95

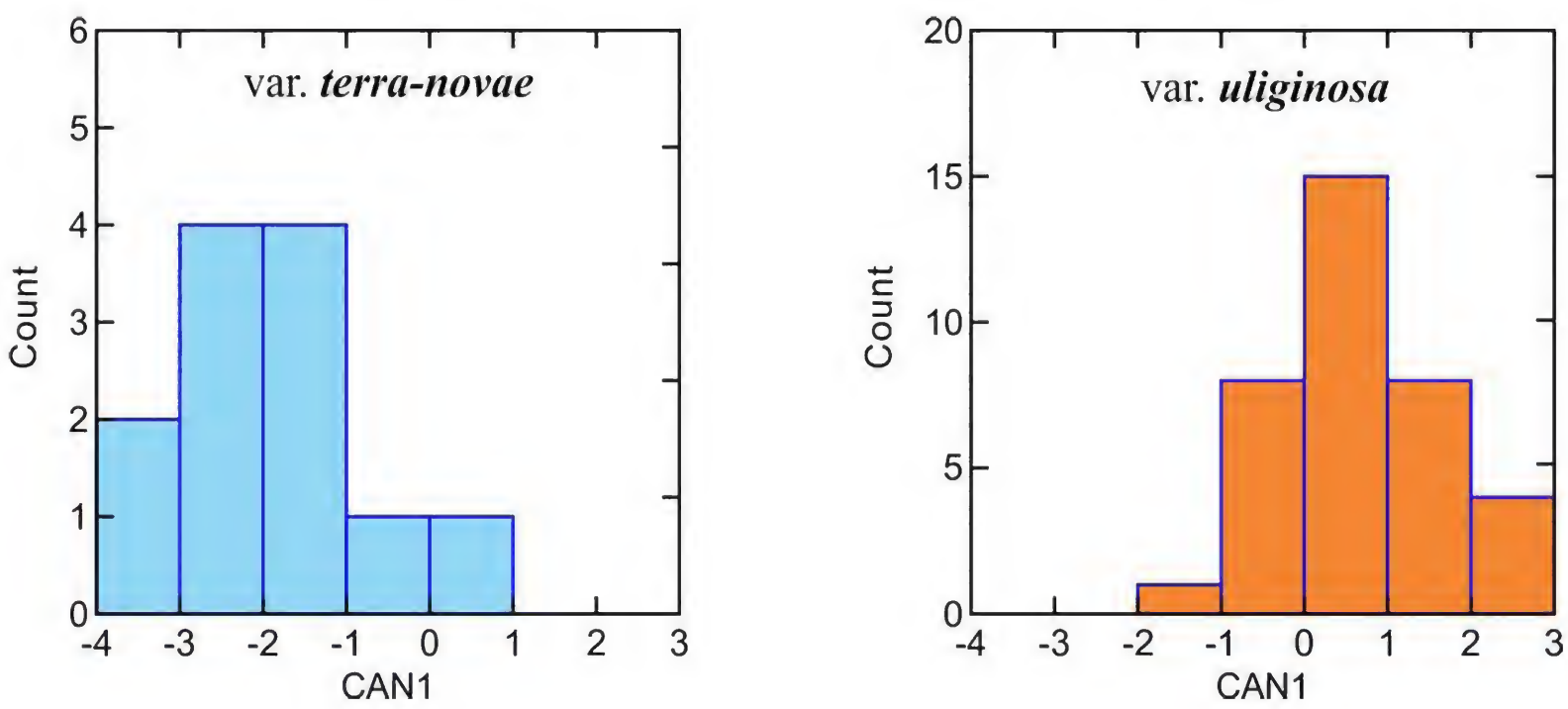

Figure 20. Histograms of canonical scores (CAN1) for *S. terrae-novae* (left) and *S. uliginosa* (including *S. purshii*; right)

Analysis 11: Analysis of S. purshii and S. terrae-novae

In the STEPWISE discriminant analysis of 32 specimens of two species/varietal level a priori groups (*S. purshii* and *S. terrae-novae*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (33.98), mid series phyllary width (15.29), and number of ray florets (10.66). Lower inflorescence branch length was not selected as strongly discriminating (0.03). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago purshii* and *S. terrae-novae* had an F-to separate value of 22.924 (Wilks' lambda = 0.2893 df = 3 1 30; Approx. F= 22.9243 df = 3 28 prob = 0.0000).

In the Classificatory Discriminant Analysis of 32 specimens of the two species/variety level a priori groups (*S. purshii* and *S. terrae-novae*) plus 1 specimen of *S. terrae-novae* only included a posteriori percents of correct a posterori assignment to the same a priori group were 95% and 90%. The Classification matrix and Jackknife classification matrix are presented in Table 20. Twenty-one of the 22 specimens of the *S. purshii* a priori group (95%) were assigned a posteriori into the *S. purshii* group; 19 specimens with 97-100% probability, 1 specimen with 77% probability, and 1 specimen with 56% probability (2). One specimen of the *S. purshii* a priori group was assigned to *S. terrae-novae* with 91% (*Dutilly 11417* MT from the Mistassini Lake region of Québec; a 39 cm tall shoot with long strictly ascending lower inflorescence branches). Nine of the 10 specimens of the *S. terrae-novae* a priori group (95%) plus 1 specimen of *S. terrae-novae* only included a posteriori were assigned a posteriori into the *S. terrae-novae* group; 9 specimens with 92-100% probability and 1 specimen with 72% probability. One specimen of the *S. terrae-novae* a priori group was assigned to *S. purshii* with 53% (*Rouleau 5165* MT from Newfoundland; the second sheet of this number; a 35 cm tall shoot).

Table 20. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	***purshii***	***terrae-novae***	**% correct**
purshii	21	1	95
terrae-novae	1	9	90
Totals	22	10	94

Jackknifed classification matrix

Group	***purshii***	***terrae-novae***	**% correct**
purshii	21	1	95
terrae-novae	1	9	90
Totals	22	10	94

Histograms of canonical scores (CAN1) for 33 individuals of *S. purshii* and *S. terrae-novae* are shown in Fig. 21. The eigenvalue on the first axis was 2.456.

DISCUSSION

The results from the discriminant analyses support the recognition the following taxa in the *Solidago uliginosa* complex: *Solidago simulans, S. uliginosa* var. *peracuta*, *S. uliginosa* var. *terrae-novae*, and *S. uliginosa* var. *uliginosa*. A key to all taxa in *Solidago* subsect. *Maritimae* is presented at the end of the discussion. Comments on each taxon accepted are present below.

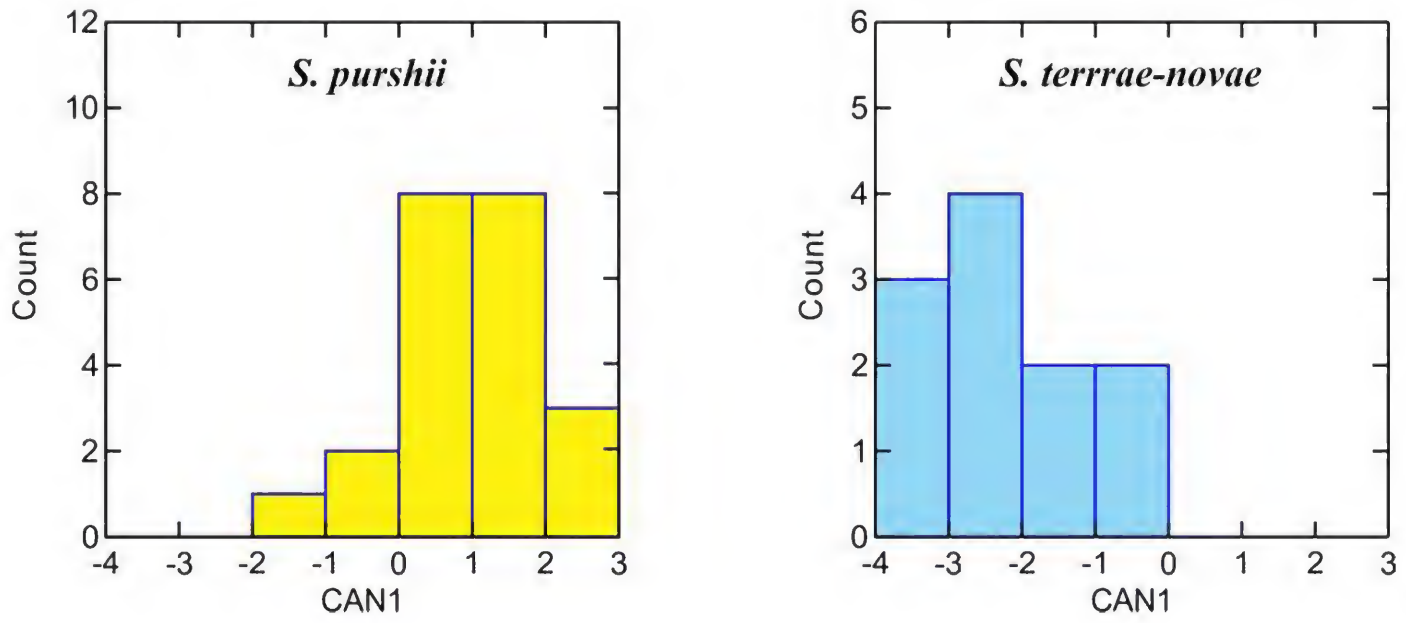

Figure 21. Histograms of canonical scores (CAN1) for for *S. purshii* (left) and *S. terrae-novae* (right).

Excluding Analysis 1, in the five analyses that included *Solidago austrina* and *S. simulans* as separate taxa, the mean percent of correct a posteriori placement for both species was 87.6% with ranges of 85-92% for the former and 81-94% for the latter. *Solidago austrina* had means of 24.3 leaves on the upper 25% of the stem below the inflorescence, 3.2 rays, and 10.4 disc florets. *Solidago simulans* had means of 13.5 leaves on the upper 25% of the stem below the inflorescence, 3.2 rays, and 7.4 disc florets. *Solidago uliginosa* s.l. had means of 8.3 leaves on the upper 25% of the stem below the inflorescence, 5 rays, and 6.2 disc florets. The greater density of leaves (internode length versus leaf length) on stems of *S. austrina* and its allopatric distribution separate the species from members of the *S. uliginosa* complex. *Solidago austrina* was treated as a member of the *S. stricta/S.virgata* complex by Semple et al. (2016b).

Results of the Analyses 3 and 4 indicate that *Solidago simulans* and *S. uliginosa* both sensu stricto and sensu lato can be distinguished with high probability by sometimes subtle technical differences. The length of mid series phyllaries, number of ray florets, and the length of the lower longer inflorescence branches were selected in both analyses as most important in separating the two taxa, but the latter trait was more important in Analysis 4 including just var. *uliginosa* individuals; number of disc florets was the fourth trait selected. In Analysis 3, *S. uliginosa* included individuals of var. *peracuta* (*S. purshii*), var. *terrae-novae*, and var. *uliginosa* with the result that the number of nodes in the upper 25% of the stem was selected as the third most significant trait and inflorescence branch length was fourth in separating *S. simulans* and *S. uliginosa* s.l. Differences in numbers of upper stem leaves is a reflection of the fact that individuals of *S. uliginosa* tend to be shorter in northern portions of the range and thus have fewer nodes per stem overall than individuals from more southern populations. This is also true if *S. austrina* is added to the comparison because it is both taller and more southern in distribution than *S. simulans* and *S. uliginosa*. In Analysis 2, number of nodes in the upper 25% of the stem was selected as the third most significant trait in separating *S. austrina*, *S. simulans* and *S. uliginosa* s.l., but *S. austrina* has more congested leaves over the whole stem than the other two species. The number of nodes on the upper 25% of the stem below the inflorescence was the same for both *S. simulans* and *S. uliginosa* var. *uliginosa*: on average 13 nodes (leaves) for both taxa were present on the upper 25% of the stem. The mean length of mid stem phyllaries was 3.4 mm for samples of *S. simulans* and 2.8 mm for *S. uliginosa* var. *uliginosa,* but total involucre length at flowering was essentially the same, 5.06 mm and 4.93 mm, respectively. The difference in numbers of florets was also critical but small: averaging 3.2 rays and 7.5 disc florets for samples of *S. simulans* and 4.5 rays and 5.8 disc florets for samples of *S. uliginosa* var. *uliginosa*. On average, *S. simulans* has fewer rays and more discs than *S. uliginosa* var. *uliginosa*. *Solidago simulans* also had slightly longer, wider and more serrate basal leaves and less hairy but longer ray and disc floret ovaries at flowering than *S. uliginosa* var. *uliginosa* on average, but the traits were not

selected as significant in discriminating the two taxa. Such differences do indicate that the two taxa differ on average in multiple traits even if the ranges of variation overlap considerably. Overall, we conclude that it is useful to recognize *S. simulans* as a distinct southern species in the *S. uliginosa* complex.

Included in the *Solidago simulans* a priori group was a problematic specimen, *Chapman s.n.* NY from middle Florida. It was provisionally assigned to *S. simulans* for the analyses; it was not assigned to species on the original collection label or the FNA label; Max Medley annotated it as *Solidago* cf. *uliginosa* in 1992; JCS annotated the species to genus only in 2012. Middle Florida is way outside the range of *S. uliginosa* and outside the range of *S. simulans*, but not far outside the range of *S. austrina* (Fig. 10). Two shoots are present on the herbarium sheet. The lower leaves have petiole bases that are slightly expanded and are obviously serrate. The inflorescences are short and the lower branches are not elongated; one is somewhat secund. The specimen was assigned a posteriori into *S. uliginosa* in Analysis 1 (92%; 6% to *S. simulans*, and 1% to *S. austrina*), Analysis 2 (80%), Analysis 3 (52%), Analysis 4 (53%), and Analysis 7 (73%) and to *S. terrae-nov*ae in Analysis 6 (62%). If the specimen is correctly identified as *S. uliginosa*, then the question is how did that species get to central Florida in the mid 1800s. It makes more sense that it is an outlier in *S. austrina* disjunct from the Tallahassee area of the Florida Panhandle; superficially it might fit into that species morphologically, but the results of the analyses indicated otherwise. Alternatively, the collection was labeled in New York with the wrong label and is in fact from much further north. *Chapman s.n.* (NY) from middle Florida remains problematic. DNA analysis might clarify the identification.

Two collections observed online from the same area in southwestern Virginia indicate the problem with easily separating *Solidago simulans* and *S. uliginosa*. *Bentley 337* (VPI) from Big Spring Bog, 2615 ft. (797 m), Grayson Co., Virginia has a small inflorescence with short ascending lower branches. *Ogle s.n.* (VPI) from The Glades, Grayson Co., Virginia has a large inflorescence with ascending-diverging lower branches. Both collections were identified as *S. uliginosa* and posted on line under that name on SERNEC. *Krouse s.n.* (NCU) from a bog near the top of Bluff Mt. (ca. 1550 m), Ashe Co., North Carolina has an inflorescence similar to *Ogle s.n.*, but with more mature heads on the lower branches; it was placed a posteriori in Analysis 3 of this study into *S. simulans* with 62% probability. Thus, it is likely that the two southwest Virginia collections are also *S. simulans*, although *Bentley 337* has an inflorescence more typical of *S. uliginosa* var. *peracuta*, which does not occur in Virginia. The next geographically nearest collection observed from Virginia was *Bills s.n.* (VPI) from Allegheny Mt., Highland Co., Virginia; this has an inflorescence similar to that of *Downs 6769* (NCU) from Grant Co., West Virginia which was placed a posteriori in Analysis 3 into *S. uliginosa* with 89% probability. There is a gap of multiple counties separating the southern most collections of *S. uliginosa* var. *uliginosa* in the Appalachian Mts. of Virginia and West Virginia from the northern most collections of *S. simulans* in the Appalachian Mts. of northern North Carolina and adjacent southwestern Virginia. Both species extend eastward at lower elevations onto the Piedmont and all of these lower elevation collections are treated here as *S. uliginosa* in Virginia and as *S. simulans* in North Carolina.

The results of Analyses 5-11 support recognition of three varieties within *Solidago uliginosa*, although an argument could be made for separating the generally more southern tetraploid var. *uliginosa* as a separate species from a more northern mostly diploid *S. purshii* including var. *peracuta* and var. *terrae-novae*. We choose not to do so because many of the differences are the result of ploidy level gigas effect and the shorter growing season for more northernly distributed plants resulting in shorter stems with generally shorter inflorescences. Ploidy level differences alone are not considered to be a basis for separating species in *Solidago* because it is likely that in most cases polyploids evolved as autopolyploids within single taxa, and potentially more than once, e.g. tetraploids in *S. nemoralis* Ait. ssp. *nemoralis* (Brammall and Semple 1990). If ploidy differences are

the base for separating diploids from tetraploids and from hexaploids into separate species, then in many cases only traits known to be influenced by ploidy level (e.g., involucre height, disc corolla length, ovary/cypsela body and pappus length) would have to be used to separate many two ploidy level and three ploidy level taxa into two or three unreliably distinguishable species: e.g., *S. altissima* L. var. *gilvocanescences* (Rydb.) Semple into three species, *S. altissima* L. var. *pluricephala* M.C. Johnston into two species, *S. gigantea* Ait. into three species, *S. missouriensis* Nutt. into two or more species, *S. velutina* DC. into three species, and *S. virgata* into three species, to name just a few examples of many in *Solidago* (Semple 2016).

The three varieties of *Solidago uliginosa* (var. *peracuta*, var. *terrae-novae*, and var. *uliginosa*) are best separated on inflorescence branching pattern traits. In all three varieties, taller stems tend to have the largest inflorescences. The typical race var. *uliginosa* usually has longer diverging inflorescence branches, although small inflorescences often have lower branches too short to show much divergence away from the main axis with stems short to very tall (52-136 cm tall). The var. *uliginosa* is allopatric in the southern part of its range but is sympatric in the parts of its range that extends north along the Maine coast in the east and in the Great Lakes area near the shores of Lake Huron and Lake Michigan near populations of var. *peracuta* in the western portion of the range. Only tetraploids are known in var. *uliginos*a, which means involucres and cypselae will be somewhat larger than found in the other two varieties. Field and garden grown vouchers for the tetraploids reported from Oka, Québec (Beaudry and Chabot 1959), have inflorescences typical for var. *uliginosa*, even though this location is well within the range of var. *peracuta*. Several dozen diploid counts for var. *peracuta* have been made in eastern Ontario, southern Quebec and adjacent New York and Vermont. Perhaps the Oka area tetraploids were introduced from the Great Lakes area. Diploids occur throughout the range of var. *peracuta* (Fig. 10), which includes very short to very tall stems (9-102 cm tall) with small to larger inflorescences with lower branches strongly ascending and diverging only slightly from the main axis; a few tetraploids have been reported from near James Bay in Québec (Beaudry and Chabot 1959; Beaudry 1969) and the field and garden grown vouchers have either typical inflorescences for var. *peracuta* or ones with rather long ascending lower branches. The inflorescences of individuals of var. *terrae-novae* (ploidy level unknown) have long lower branches that ascend and are somewhat divergent making the inflorescence often nearly as wide as tall and somewhat corymbiform in overall shape with stems generally very short to short (8-43 cm tall). This can be obvious even in small shoots with small inflorescences (Fig. 6). Intermediates with var. *peracuta* occur and inflorescence branching pattern can grade from one form to the other. The var. *terrae-novae* is aptly named as it is known only from Newfoundland and mostly from the southern portion of the province. Cronquist (1968) noted that plants of var. *peracuta* had "leaves seldom much toothed", but numbers of serrations of middle and upper leaves were not selected as significant traits in separating the varieties in our Analysis 8. In fact, for mid stem leaves of var. *peracuta* the mean number of margin serrations on one side of the leaf was higher (8.74) than for var. *uliginosa* (4.77), but slightly lower than for var. *terrae-novae* (9.73).

Key to taxa in *Solidago* subsect. *Maritimae*

[Short plants with short inflorescences can be a problem to identify when traits or large inflorescences are critical in separating similar species.]

1. Disc florets 10-20; central Mexico ..... **Solidago paniculata**
1. Disc florets 3-12; Gulf coastal and southern Mexico, eastern Canada and USA.
    2. Upper leaves somewhat reduced from mid and lower leaves.
        3. Middle stem leaves broadly lanceolate to ovate; Azores, Bermuda ..... **Solidago azorica**
        3. Middle stem leaves narrowly lanceolate; coastal from Newfoundland to northern North Carolina, introduced inland along heavily salted roads in the eastern USA ..... **Solidago sempervirens**

2. Upper leaves much reduced from lower leaves.
  4. Upper stem leaves not congested, relatively few.
    5. Inflorescence with a few long spreading branches well below the apex; basal leaves serrate; piedmont of North Carolina to panhandle Florida ..... **Solidago gracillima**
    5. Inflorescence either elongate and narrow or lower branches variously ascending to spreading, many and grading in length into short upper branches.
      6. Lower and mid stem leaves entire; mountains in Chiapas, Mexico, Guatemala, Belize ..... **Solidago maya**
      6. Lower and mid stem leaves serrate; eastern Canada and USA.
        7. Rays averaging 3, discs averaging 8; southwestern Virginia to eastern Tennessee in mountains south to northern Georgia, scattered in eastern piedmont of southern North Carolina ..... **Solidago simulans**
        7. Rays averaging 5, discs averaging 6; Newfoundland to northern Virginia west to Hudson's Bay and southeastern Manitoba south to central Illinois ..... **Solidago uliginosa**
          8. Inflorescence somewhat corymbiform to compressed secund and nearly as wide as long; Newfoundland ..... **S. uliginosa** var. **terrae-novae**
          8. Inflorescence not somewhat corymbiform and usually much longer than wide.
            9. Inflorescence narrow, elongated and branches short or strongly ascending; eastern Canada northern USA ..... **S. uliginosa** var. **peracuta**
            9. Inflorescence branches elongated and divergent; coastal Maine to coastal Lakes Huron and Michigan to Illinois and Virginia ....**S. uliginosa** var. **uliginosa**
  4. Upper stem leaves congested, relatively many.
    10. Basal and lower stem leaves serrate; inflorescence sometimes secund.
      11. Lower inflorescence branches of large plants spreading arching, many; outer piedmont North Carolina to Alabama north to Tennessee and south to Tallahassee area in Florida ..... **Solidago austrina**
      11. Lower inflorescence branches of large plants ascending diverging, few; sandy pine barrens New Jersey to Virgiana south to North Carolina on inner coastal plain/ Piedmont fall line; rarely further south ..... **Solidago stricta**
    10. Basal and lower leaves not serrate; inflorescence always narrow, sometimes secund.
      12. Inflorescence apex slightly secund (sometimes not in Louisiana and Texas); leaves somewhat to obviously fleshy; outer coastal plain near brackish waterways, along coast Maryland to Tabasco, Mexico, rare in Bahamas and Cuba ..... **Solidago mexicana**
      12. Inflorescence never with secund apex; outer coastal plain.
        13. Disc florets averaging 14 (10-21); basal and lower stem leaves averaging 31 (22-37) mm × 5.4 (3-8) mm; outer coastal plains North Carolina and adjacent South Carolina ..... **Solidago pulchra**
        13. Disc florets averaging 7-8 (4-12); basal and lower leaves averaging 56-60 (17-155) mm × 5.5-9.2 (1-27) mm.
          14. Basal and lower stem leaves oblanceolate to rarely obovate; outer coastal plain North Carolina to eastern Louisiana ..... **Solidago virgata**
          14. Basal and lower stem leaves linear; south Florida and Keys ..... **Solidago chrysopsis**

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AN ASSESSMENT OF INVASIVE STATUS OF NON-NATIVE VASCULAR PLANT SPECIES IN OKLAHOMA

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ABSTRACT

The proliferation of non-native invasive species globally has created ecologic and economic duress. The Convention on Biological Diversity has called for the identification and prioritization of invasive non-native species by 2020. Although numerous ranking methodologies exist to meet this goal, the data required are often lacking for most taxa in a region. I used the Fundamental Invasiveness Index to assess the invasive potential of 436 non-native species of vascular plants in Oklahoma. It evaluates taxa based on five criteria: (1) nativity, (2) approximate date of introduction, (3) current geographic distribution, (4) ecological/reproductive behavior, and (5) basic habitat and growth. Seventeen species are ranked as F1, 115 as F2, and 305 as F3. *Amaranthus graecizans* and *Glinus lotoides* are the first recorded non-native vascular plants in Oklahoma. Eight counties have ten or more first reports of a non-native taxa. Thirty-four species are designated as Watch. The Fundamental Invasiveness Index provides great facility for evaluating a large number of non-native taxa.

The ecologic and economic impact of non-native invasive species has been the subject of intense study in recent decades and the literature on the subject is burgeoning (see Pysek & Richardson 2010; Lowry et al. 2013; Dueñas et al. 2018). The Convention on Biological Diversity included non-native invasive species in the Strategic Plan for Biodiversity as one of the 20 Aichi Targets. Target 9 states that "By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated and measures are in place to manage pathways to prevent their introduction and establishment" (Leadley et al. 2014). Target 9 recognizes that not all non-native species that are established in a geographic locale are invasive. For example, the U.S. Fish and Wildlife Service (2019) estimates that of 50,000 non-native species that occur in the USA, only 4,300 (11.6%) are invasive. In this paper, I assess the invasive potential of non-native vascular plants known to occur in the state of Oklahoma using the Fundamental Invasiveness Index (FNI) developed by Nesom (2009).

A bewildering lexicon has evolved around the terms non-natives species and invasive. The definitions I use here are derived from Section 1 of Presidential Executive Order 13112 (1999). For example, my use of "non-native species" is synonymous with the term "alien species" as defined in the Executive Order: "Alien species means, with respect to a particular ecosystem, any species, including its seeds, eggs, spores, or other biological material capable of propagating that species, that is not native to that ecosystem." The terms introduction ("the intentional or unintentional escape, release, dissemination, or placement of a species into an ecosystem as a result of human activity") and invasive species ("an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health") follow the Executive Order.

METHODS

Government agencies and NGOs have developed and/or adopted frameworks for evaluating invasive potential to assist conservation biologists and land managers in recognizing which non-native species pose a current or potential threat as an invasive; the NatureServe (Morse 2004)

Invasive Species Impact Rank and the New York Non-Native Plant Assessment (2019) are two of many examples. The majority of these frameworks require access to extensive geographic and life history data that often is not complete or readily available. In many cases, the data required are lacking for some taxa. This presents a challenge for the assessment and ranking of non-native species in a state or regional flora. The Fundamental Invasiveness Index (Nesom 2009) is a readily accessible framework for the assessment of invasive potential of a large pool of non-native species in a flora. Each non-native taxon is evaluated based on five categories: (1) nativity, (2) approximate date of introduction, (3) current geographic distribution, (4) ecological/reproductive behavior, and (5) Basic habitat and growth (Nesom 2009). Each species or taxon is then evaluated and assigned to one of four categories (Nesom 2009):

> **F1:** Invasive in both disturbed and natural habitats, negatively affecting native species or natural biodiversity by altering native vegetation and habitats or by outcompeting or hybridizing with native species, or, invasive into agricultural habitats and causing significant economic damage, including woody, herbaceous, and aquatic species.
> **F2:** Abundant in number and widespread, commonly invasive in disturbed habitats, much less commonly in natural habitats, subdivided into woody, herbaceous, and aquatic species.
> **F3:** Relatively few in number, known from relatively few localities, usually in disturbed habitats, subdivided into woody and herbaceous species.
> **F4:** Status unknown

I initiated this project by generating a list of non-native vascular plants from the Oklahoma Vascular Plants Database (OVPD 2019). The OVPD contains >240,000 records, each representing a voucher deposited in one of eight in-state herbaria. The OVPD captures all information provided by the collector on the voucher label, which is parsed into Darwin Core (Wieczorek et al. 2012) fields. The OVPD also contains the annotation history of each voucher. Some taxa on the preliminary list are ornamental or other cultivated plants. These were discarded if the collector indicated that the voucher was planted or cultivated. If not indicated as such, the taxon was retained on the list.

Nativity was determined using Taylor and Taylor (1994) and USDA Plants (2019). Approximate date of introduction is defined as the specimen of a non-native species in the OVPD with the earliest collection date. It is recognized that the non-native species probably arrived in the state long before the first collection, but herbarium records are the closest approximation of arrival times available. For example, the Robert Bebb Herbarium at the University of Oklahoma (OKL) is the oldest herbarium in the state and was therefore the primary source for approximate date of introduction. Founded in1893 by Professor Edwin DeBarr, at which time it housed 250 specimens from Oklahoma, OKL grew to 4,000 specimens by 6 January 1903. Sadly, OKL was destroyed by fire in that year and all specimens were lost (Rice & Cross 1990). Although the OVPD does contain records from 1894 to the present, the destruction of OKL in 1903 may resulted in the loss of vouchers with earlier approximate dates of introduction. Therefore, it seemed prudent to review floristic lists from Oklahoma that predated the fire, the most comprehensive of which are Holzinger (1892), Olive (1895), and Bogue (1900). Only the *Annotated catalogue of the ferns and flowering plants of Oklahoma* by Ernest Everett Bogue included non-native plant species. Bogue, a botanist and entomologist at the Oklahoma Agricultural Experiment Station (located in Guthrie, Oklahoma Territory), based his catalog upon specimens maintained at the Station. Professor Joseph W. Blankenship, who was a member of the faculty at Montana State College of Agriculture and Mechanical Arts, assisted Bogue with identifications and contributed information from his personal collections made in Oklahoma Territory (Bogue 1900). There are no records in the OVPD bearing either the name Bogue or Blankenship.

County distribution records in the OVPD were the basis for current geographic distribution. Ecological/reproductive behavior in Oklahoma and in other regions was based on published literature, information provided herbarium collection labels, and expert knowledge. Basic habitat and growth form (forb, graminoid, vine, or woody) information was determined using Taylor and Taylor (1994) and USDA Plants (2017). The taxonomy follows the ITIS (2019).

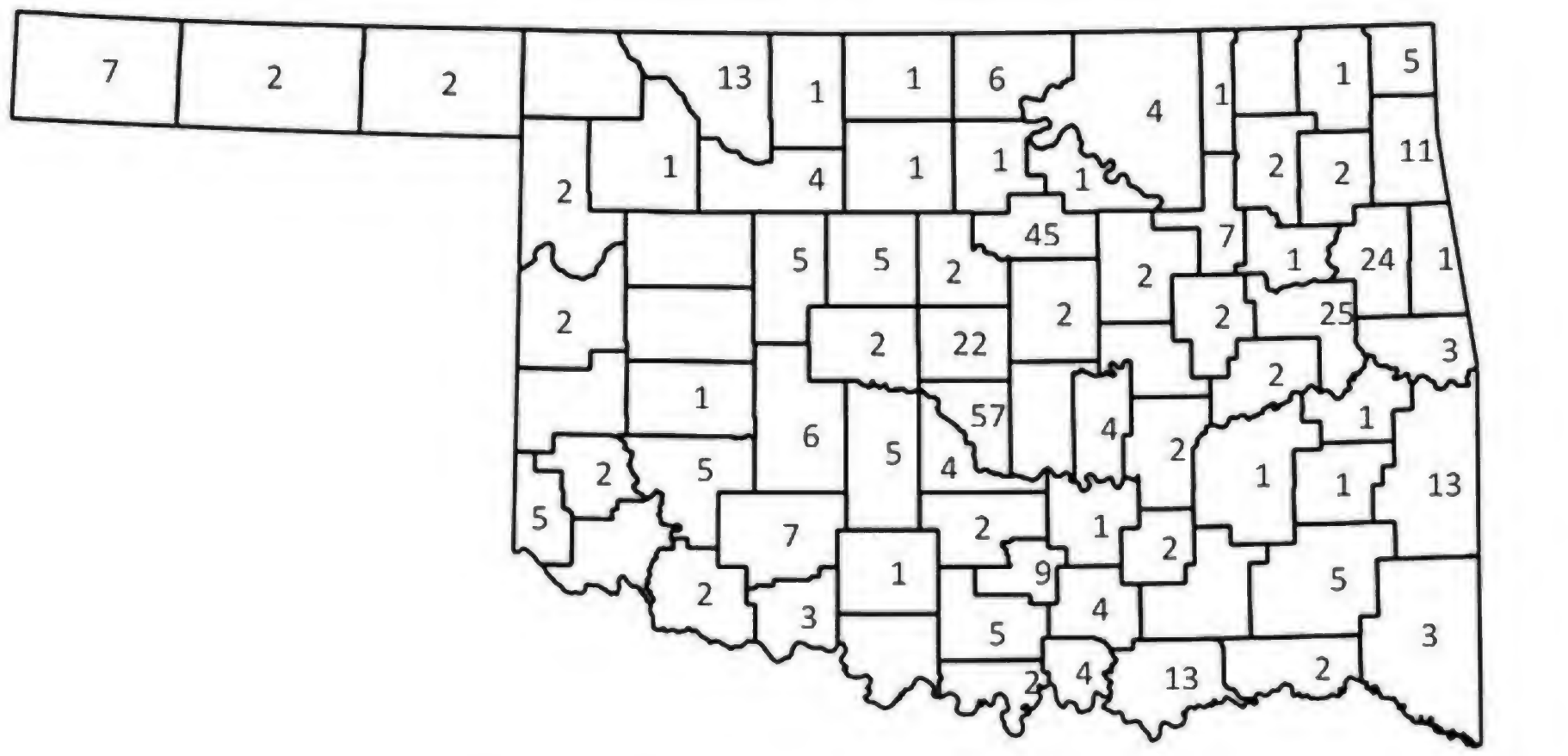

Figure 1. A count of approximate first date of introduction by county for non-native vascular plant taxa based upon records in the Oklahoma Vascular Plant Database (2019).

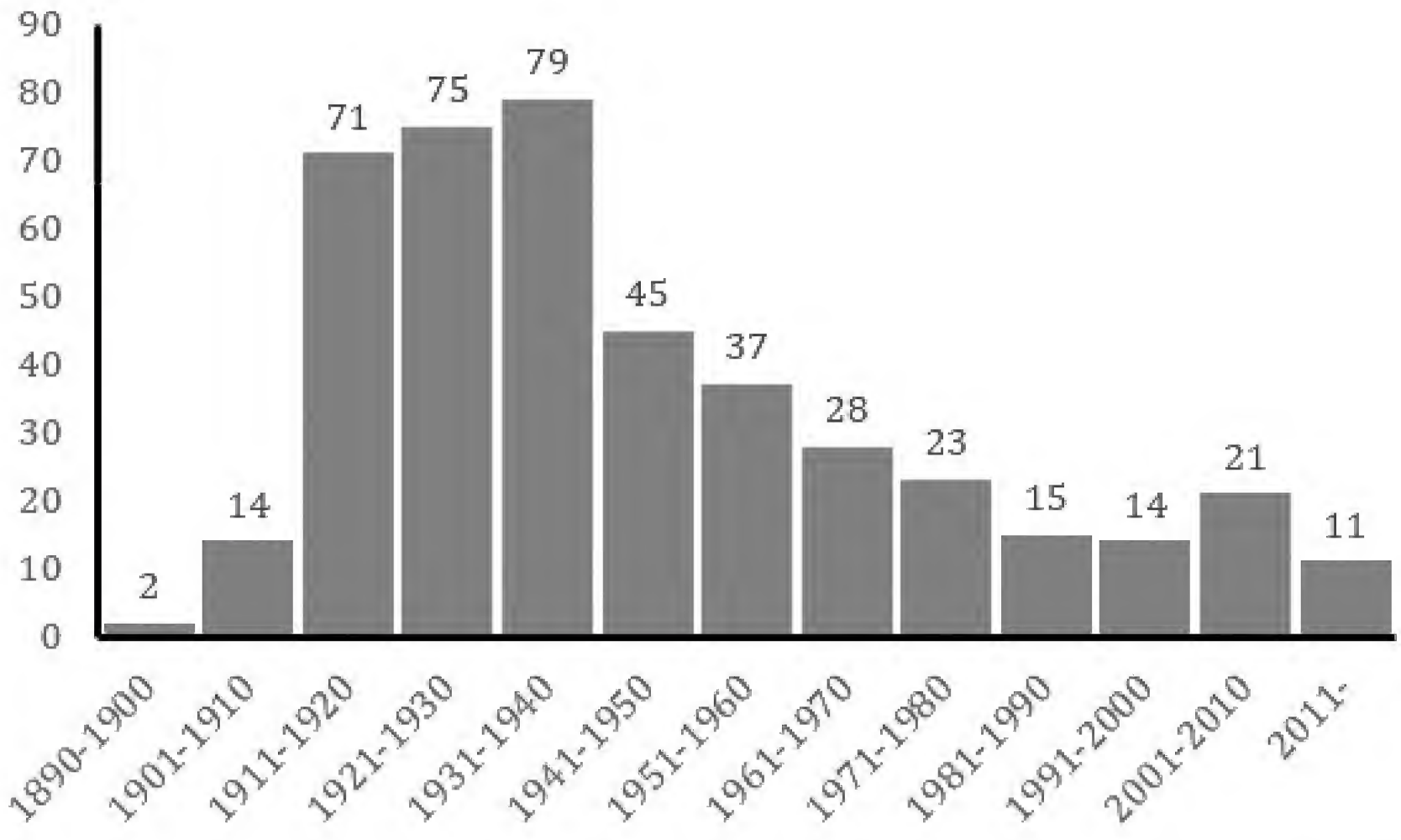

Figure 2. A count of approximate first date of introduction by year for non-native vascular plant taxa based upon records in the Oklahoma Vascular Plant Database (2019).

RESULTS AND DISCUSSION

A total of 436 species in 265 genera and 73 families were assessed and assigned a Fundamental Invasiveness Index score (Table 1). Four families have 30 or more non-native taxa: Asteraceae (n=37), Brassicaceae (n=32), Fabaceae (n=46), and Poaceae (n=86). The five genera containing the most species evaluated are *Bromus* (n=10), *Eragrostis* (n=8), *Medicago* (n=6), *Rumex* (n=6), *Trifolium* (n=11), and *Veronica* (n=6). In terms of life history, 216 are annuals, 35 biennials, 185 perennials, and among life history categories 305 (including two ferns) were forbs, 90 are graminoids, 40 trees or shrubs, and eight vines. The number of taxa in each Fundamental Invasiveness Index rank are F3 = 294, F2 = 119, F1 = 21.

Amaranthus graecizans and *Glinus lotoides* are the first vouchered non-native vascular plants in Oklahoma; both were collected in 1894. Neither, however, can be confidently attributed to a county of collection. Seven specimens dating from 1902-1930 also lacked a county of collection. This represents one of two challenges when working with older collections: (1) lack of geographic location and/or (2) no collection date recorded on the label. In regard to the former, location of the collection was either not provided on the label or was confounded by changes in the internal geography of the state. The specimen of *Glinus lotoides* was collected by Benjamin Franklin Bush of Missouri on 30 July 1894, which is prior to statehood (Oklahoma entered the Union in 1907). It was one of several vouchers labeled as "Plants of Indian Territory" at OKL and the Oklahoma State University herbarium (OKLA). The location is listed as "Verdigris," which either refers to the settlement of Verdigris (present day Rogers County) or a location along the Verdigris River, which passes through several counties. Less problematic is the Bush specimen of *Amaranthus graecizans,* collected at a location reported as Sapulpa, Creek Nation, Indian Territory. At the time of the collection, Sapulpa was part of the Okmulgee District of the Creek Nation, but after statehood it became the county seat for Creek County.

First occurrences are reported from 67 of the 77 counties in Oklahoma (Figure 1). Eight counties have ten or more first reports of a non-native taxon: Cleveland (n=57), Payne (n=45), McCurtain (n=40), Muskogee (n=25), Cherokee (n=24), Oklahoma (n=22), Bryan (13), LeFlore (n=13), and Woods (n=13). The leading two counties are home to the University of Oklahoma and Oklahoma State University, respectively. Five species had the same year of approximate date of introduction but specimens reported from two counties: LeFlore and Pushmataha (*Cardamine hirsuta*, 1968), Kiowa and Tilman (*Glaucium flavum*, 1985), Cleveland and Murray (*Ipomoea purpurea*, 1919), Adair and Delaware (*Leucanthemum vulgare*, 1938), and Cleveland and Oklahoma (*Lythrum salicaria*, 1993). The most broadly distributed of the non-native species are *Capsella bursa-pastoris* and *Echinochloa crus-galli* (both ranked F2), reported from 72 of the 77 counties respectively.

The year 1913 has the most approximate dates of introduction (n=46) for non-native vascular plants, with subsequent peaks in 1927 and 1940 (15 records each; Figure 2). In the 123 years since the first documentation of a non-native vascular plants in Oklahoma, there have been only 23 years without a first occurrence record.

All records for 1913 were collected by George Walter Stevens (1868-1936), a faculty member at the State Normal School in Alva (now Northwestern Oklahoma State University) from 1904 to 1912 and director of the State Botanical Survey (which is defunct) in 1913 (Lawson et al. 1978). He and four assistants conducted five collecting expeditions, each to a different region of Oklahoma, from 6 April to 20 September 1913, resulting in some 4,600 specimens (Goodman et al. 1978). He later completed the first flora of Oklahoma (Stevens 1916).

As mentioned earlier, two vexing aspects of this research have been the lack of location information and/or collection date for a voucher. In the case of *Matricaria recutita*, only two vouchers exist; one lacks a collection date, the other location information. The only specimen of

Tanacetum vulgare, collected by Celeste Whaley in Delaware County, lacks a collection date. Many vouchers collected by Stevens, an important source of early 20th century botanical material for Oklahoma, often lack collection dates. Two examples are his collections of *Cyperus rotundus* and *Heliotopium indicum* from McCurtain County, which was not included in the itinerary of the 1913 expeditions. To ascertain the year of collection, I determined that collection numbers for Stevens work in McCurtain County range from 3745 and ends with 3888. A collection date accompanies only one of those specimens: *Asplenium platyneuron*, collection number 3857, 28 May 1916. *Cyperus rotundus* and *H. indicum* bear the collection numbers 3745 and 3752, so the approximate date of introduction for these two species is indicated as 1916. Otherwise, the approximate date of introduction for *C. rotundus* is 1941, based on the specimen collected by C. Smith and W. Randel from Pontotoc County, and 1919 for *H. indicum*, from a specimen by R.E. Jeffs from LeFlore (Appendix 1). Of course, this would change the first county of collection as well.

Based on the species list provided by Bogue (1900), there were 27 species for which the approximate date of introduction was earlier than the specimen in the OVPD (Appendix 2). Actual collection dates were not provided by Bogue. For example, the first collection in the OVPD of *Sorghum halepense* was by Stevens on 21 June 1913 from Harmon County. *Sorghum halepense* appears in Bogue's catalog for Oklahoma Territory with the note "introduced from Texas. Considered by many as a most troublesome weed and by others as a most valuable forage plant. It is very tenacious… ."

Bogue (1900) also reported *Anredera baselloides* as occurring in Oklahoma Territory, noting "Determined by J.W. Blankinship, this is the first record north of its appearance north of Mexico. Collected only once by F.M. Greiner at Stillwater. Have not been able to find plants since the first collection," nor has it been found since. Also included in his list is *Canavalia ensiformis* (L.) DC. "a volunteer in sandy soil along the Cimarron" River. There are no records of either plant in the OVPD.

Of the 436 taxa assessed, only 17 (4%) are ranked as F1. The majority of species are ranked as F3 (n= 305, 70%); F2 species account for 26% (n=115). Thirty-four species are designated as Watch (W): F3W=15, F2W=20. The watch list for Oklahoma Invasive Plants Council lists 29 species, of which 26 species are designated as Watch species here. It should be noted that the watch designation in this research is not intended to contradict or call in to question the OKIPC watch list.

CONCLUSIONS

Existing frameworks for evaluating and ranking the potential for invasive behavior by non-native species can be challenging when employed for a large number of taxa. In this research, the Fundamental Invasiveness Index provided great facility for evaluating numerous species of non-native taxa. Pairing the Fundamental Invasiveness score with a Watch designation, as recommended by Nesom (2009), provides an understanding of whether the taxa possesses a moderate or high level threat. Watch species in this research are F2 and F3 due to the limited number of geographic locations reported. For example, *Hydrilla verticillata* is ranked as F2W, primarily due to the low number of occurrences within the state. The same is true for *Onopordum acanthium* and *Murdannia keisak,* both ranked as F3. As with all ranking systems, the Fundamental Invasiveness score should be reevaluated for each species at regular intervals. If the number of populations reported increases, the Fundamental Invasiveness Index score could change. But to have timely and relevant data requires funds allocated by agencies for continued inventory.

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APPENDIX 1

Fundamental Invasiveness Index scores for alien vascular plants known to occur in Oklahoma. Each entry consists of the assigned Fundamental Invasiveness Index (F1-F3. Note that a "W" immediately following the F-rank indicates a Watch species [i.e., F1W]), life history (P=perennial, A=annual, B=biennial), growth habit (F=forb, G=graminoid, V=vines, W=woody), CO=number of counties from which the taxon is currently known to occur, the name of the county from which the taxon was first reported (in some cases, first report may have been from two counties in the same year. Unknown indicates that the collector did not provide the county of location), and the date of first collection. Symbols: † = species on the Oklahoma Invasive Plant Council Watch List (www.okinvasives.org/watch-list-1); * = designated as a noxious aquatic plant by the Oklahoma Department of Wildlife Conservation; # = designated as a noxious weed by the Oklahoma Department of Agriculture, Food, and Forestry. The taxonomy follows the ITIS (2017).

ACORACEAE
Acorus calamus L. - F1, P, F, CO=5, Cleveland, 1937

AMARANTHACEAE
Alternanthera caracasana Kunth - F3, P, F, CO=2, Cleveland, 1944
Alternanthera paronychioides A. St.-Hil. - F1, P, F, CO=1, Pushmataha, 2001
*†*Alternanthera philoxeroides* (Mart.) Griseb. - F2W, P, F, CO=3, Wagoner, 1996
Alternanthera pungens Kunth - F3, P, F, CO=1, Bryan, 1972
Amaranthus albus L. - F2, A, F, CO=33, Blaine, 1913
Amaranthus blitoides S. Watson - F3, A, F, CO=1, Woods, 1916
Amaranthus graecizans L. - F3, A, F, CO=31, Creek, 1894
Amaranthus retroflexus L. - F2, A, F, CO=37, Kingfisher, 1903
Amaranthus spinosus L. – F3, A, F, CO=35, Ottawa, 1913
Atriplex patula L. - F3, P, W, CO=4, Oklahoma, 1939
Chenopodium album L. - F2, A, F, CO=54, Blaine, 1913
Chenopodium glaucum L. - F3, A, F, CO=5, Harmon, 1926
Chenopodium murale L. – F3, A, F, CO=1, Canadian, 2006

Dysphania ambrosioides (L.) Mosyakin & Clemants - F2, A, F, CO=32, Major, 1913
Dysphania pumilio (R. Br.) Mosyakin & Clemants - F3, A, F, CO=11, McCurtain, 1930
Kochia scoparia ssp. *scoparia* (L.) Schrad. - F2, A, F, CO=25, Woods, 1913
Salsola collina Pall. - F3, A, F, CO=1, Cimarron, 1988
Salsola tragus L. - F1, A, F, CO=31, Harmon, 1913

AMARYLLIDACEAE
Allium ampeloprasum L. - F3, P, F, CO=2, Comanche, 1942
Allium sativum L. - F3, P, F, CO=10, Osage, 1959
Allium vineale L. - F3, P, F, CO=11, Payne, 1941
Narcissus jonquilla L. - F3, P, F, CO=3, McCurtain, 1978
Narcissus pseudonarcissus L. - F3, P, F, CO=1, Muskogee, 1993

APIACEAE
Anethum graveolens L. - F3, A, F, CO=6, Kingfisher, 1935
Anthriscus caucalis M. Bieb. - F3, A, F, CO=3, Canadian, 1964
Conium maculatum L. - F2, B, F, CO=15, Payne, 1934
Coriandrum sativum L. - F3, A, F, CO=2, Oklahoma, 1930

Cyclospermum leptophyllum (Pers.) Sprague ex Britton & P. Wilson - F3, A, F, CO=4, McCurtain, 1984
Daucus carota L. - F2, B, F, CO=24, Bryan, 1919
Falcaria vulgaris Bernh. - F3, P, F, CO=2, Major, 1957
Pastinaca sativa L. - F3, B, F, CO=2, Cleveland, 1924
Torilis arvensis (Huds.) Link - F2, A, F, CO=51, Muskogee, 1927
Torilis nodosa (L.) Gaertn. - F3, A, F, CO=15, Bryan, 1963

APOCYNACEAE
Catharanthus roseus (L.) G. Don – F3, A, F, CO=2, Payne, 1934
Vinca major L. - F3, P, F, CO=7, Payne, 1939
Vinca minor L. - F3, P, F, CO=3, Bryan, 1969

ARALIACEAE
Hedera helix L. F3, P, V, CO=2, Pontotoc, 1989

ASPARAGACEAE
Asparagus officinalis L. - F3, P, F, CO=18, Pottawatomie, 1923
Muscari botryoides (L.) P. Mill. - F3, P, F, CO=4, Oklahoma, 1926

ASTERACEAE
Anthemis cotula L. - F2, A, F, CO=24, LeFlore, 1914
Arctium minus Bernh. - F2, B, F, CO=17, Cherokee, 1925
Artemisia annua L. - F3, A, F, CO=7, Murray, 1936
Carduus nutans L. - F1, B, F, CO=32, Payne, 1946
Carthamus lanatus L. - F3, A, F, CO=2, McClain, 1985
Centaurea cyanus L. - F2, A, F, CO=22, Cleveland, 1928
Centaurea solstitialis L. - F3, A, F, CO=2, Creek, 1947
Cichorium intybus L. - F2, P, F, CO=11, Murray, 1945
#*Cirsium vulgare* (Savi) Ten. - F2, B, F, CO=15, Cherokee, 1951
Cosmos sulphureus Cav. - F3, A, F, CO=2, McClain, 1960
Crepis pulchra L. - F3, A, F, CO=10, Latimer, 1958
Facelis retusa (Lam.) Sch. Bip. - F3, A, F, CO=11, McCurtain, 1957
Galinsoga parviflora Cav. - F3, A, F, CO=2, Cimarron, 1967
Galinsoga quadriradiata Cav. - F3, A, F, CO=2, Cherokee, 1924
Lactuca saligna L. - F3, B, F, CO=7, Oklahoma, 1972
Lactuca sativa L. – F3, B, F, CO=3, Comanche, 1938
Lactuca serriola L. - F2, B, F, CO=51, Woods, 1913
Leucanthemum vulgare Lam. - F2, P, F, CO=20, Adair and Delaware, 1938
Matricaria discoidea DC. - F3, A, F, CO=8, Cleveland, 1930
Matricaria chamomilla L. - F3, A, F, CO=1, Pittsburg, no date available
#*Onopordum acanthium* L. - F3W, B, F, CO=1, Roger Mills, 1976
Parthenium hysterophorus L. - F2, A, F, CO=21, Garvin, 1926
Rhaponticum repens (L.) Hidalgo - F3, P, F, CO=2, Roger Mills, 1947
Scorzonera laciniata L. - F3, P, F, CO=1, Cimarron, 2014
Senecio vulgaris L. - F3, A, F, CO=6, Oklahoma, 1997
Silybum marianum (L.) Gaertn. - F3, B, F, CO=1, Blaine, 1986
Soliva sessilis Ruiz & Pav. - F3, A, F, CO=6, Marshall, 1969
Sonchus asper (L.) Hill - F2, A, F, CO=58, Cleveland, 1916
Sonchus oleraceus L. - F3, A, F, CO=7, Payne, 1912
Tagetes erecta L. - F3, A, F, CO=3, Payne, 1972

Tanacetum vulgare L. - F3, P, F, CO=1, Delaware, date unavailable
Taraxacum erythrospermum Andrz. ex Besser - F2, P, F, CO=23, Payne, 1935
Taraxacum officinale F.H. Wigg. - F23, P, F, CO=60, Cleveland, 1913
Tragopogon dubius Scop. - F2, B, F, CO=60, Oklahoma, 1939
Tragopogon porrifolius L. - F3, B, F, CO=11, Oklahoma, 1920
Tragopogon pratensis L. - F3, B, F, CO=14, Cleveland, 1926
Xanthium spinosum L. - F3, A, F, CO=3, Marshall, 1950

BORAGINACEAE
Buglossoides arvensis (L.) I.M. Johnston - F2, A, F, CO=43, Kingfisher, 1938
Cynoglossum amabile Stapf & J.R. Drumm. - F3, B, F, CO=4, McCurtain, 1930
Myosotis stricta Link ex Roem. & Schult. - F3, A, F, CO=3, Tulsa, 1957

BRASSICACEAE
†*Alliaria petiolata* (M. Bieb.) Cavara & Grande - F3W, B, F, CO=1, Delaware, 1994
Alyssum alyssoides (L.) L. - F3, A, F, CO=3, Cleveland, 1927
Arabidopsis thaliana (L.) Heynh. - F3, A, F, CO=1, McCurtain, 1941
Barbarea vulgaris W.T. Aiton - F3, B, F, CO=11, Cleveland, 1926
Brassica juncea (L.) Czern. - F3, A, F, CO=8, Cleveland, 1922
Brassica napus L. - F3, A, F, CO=5, Payne, 1940
Brassica nigra (L.) W.D.J. Koch - F3, A, F, CO=19, Cleveland, 1927
Brassica rapa L. - F3, A, F, CO=16, Cleveland, 1924
Camelina microcarpa DC. - F2, A, F, CO=42, Oklahoma, 1925
Camelina rumelica Velen. - F3, A, F, CO=14, Kingfisher, 1937
Camelina sativa (L.) Crantz - F3, A, F, CO=2, Muskogee, 1940
Capsella bursa-pastoris (L.) Medik. - F2, A, F, CO=72, Unknown, 1902
Cardamine hirsuta L. - F3, A, F, CO=27, LeFlore and Pushmataha, 1968
Cardaria draba (L.) Desv. - F3, P, F, CO=6, Payne, 1937
Chorispora tenella (Pallas) DC. - F2, A, F, CO=18, Oklahoma, 1925
Conringia orientalis (L.) Dumort. - F3, A, F, CO=10, Cleveland, 1919
Descurainia sophia (L.) Webb ex Prantl - F3, A, F, CO=29, McClain, 1937
Eruca vesicaria (L.) Cav. - F3, A, F, CO=2, Oklahoma, 1974
Erysimum repandum L. - F2, A, F, CO=44, Cleveland, 1926
Lepidium apetalum Willd. - F3, B, F, CO=3, Beaver, 1913
Lepidium campestre (L.) W.T. Aiton - F3, B, F, CO=4, Sequoyah, 1955
Lepidium densiflorum Schrad. – F3, B, F, CO=67, Unknown, 1906
Lepidium perfoliatum L. - F3, B, F, CO=3, Payne, 1937
Lepidium ruderale L. - F3, B, F, CO=1, Payne, 1934
Myagrum perfoliatum L. - F3, A, F, CO=1, Tillman, 2012
Microthlaspi perfoliatum (L.) F.K. Mey. - F3, A, F, CO=1, Kay, 1973
Nasturtium officinale W.T. Aiton - F2, P, F, CO=35, Ellis, 1913
Sinapis arvensis L. - F3, A, F, CO=16, Murray, 1934
Sisymbrium altissimum L. - F3, A, F, CO=20, Cleveland, 1919
Sisymbrium irio L. - F3, A, F, CO=1, Cleveland, 1928
Sisymbrium officinale (L.) Scop. - F3, A, F, CO=18, Cherokee, 1926
Thlaspi arvense L. - F3, A, F, CO=20, Cleveland, 1919

CANNABACEAE
Cannabis sativa L. - F3, A, F, CO=13, Lincoln, 1909
Humulus japonicus Siebold & Zucc. - F3, A, V, CO=3, Rogers and Tulsa, 2010
Humulus lupulus L. - F3, P, V, CO=9, Ottawa, 1955

CAPRIFOLIACEAE
Lonicera japonica Thunb. - F1, P, V, CO=46, Payne, 1936
†*Lonicera maackii* (Rupr.) Herder - F3W, P, V, CO=7, Woodward, 1980

CARYOPHYLLACEAE
Agrostemma githago L. - F3, A, F, CO=12, Lincoln, 1938
Arenaria serpyllifolia L. - F2, A, F, CO=52, Muskogee, 1927
Cerastium brachypetalum Pers. - F3, A, F, CO=7, Cherokee, 1952
Cerastium brachypodum (Engelm. ex A. Gray) B.L. Rob. - F2, P, F, CO=43, Mayes, 1905
Cerastium fontanum Baumg. - F2, B, F, CO=24, Cleveland, 1923
Cerastium glomeratum Thuill. - F2, A, F, CO=41, Muskogee, 1927
Cerastium pumilum W. Curtis - F3, A, F, CO=19, Muskogee, 1958
Dianthus armeria L. - F2, B, F, CO=28, Delaware, 1938
Gypsophila paniculata L. - F3, P, F, CO=2, Cleveland, 1928
Holosteum umbellatum L. - F2, A, F, CO=22, Cleveland, 1953
Petrorhagia prolifera (L.) P.W. Ball & Heywood - F3, A, F, CO=6, Cherokee, 1951
Saponaria officinalis L. - F3, P, F, CO=17, Cleveland, 1922
Scleranthus annuus L. - F3, A, F, CO=7, Marshall, 1973
Silene noctiflora L. - F3, A, F, CO=2, McCurtain, 1930
Stellaria media (L.) Vill. - F2, A, F, CO=58, Cleveland, 1915
Vaccaria hispanica (Mill.) Rauschert - F3, A, F, CO=5, Pontotoc, 1941

CELASTRACEAE
Euonymus alatus (Thunb.) Siebold - F3, P, W, CO=1, Tulsa, 1989
Euonymus bungeanus Maxim. - F3, P, W, CO=2, Kingfisher, 2013
Euonymus fortunei (Turcz.) Hand.-Maz. - F3, P, W, CO=2, Bryan, 1987
Euonymus japonicus Thunb. - F3, P, W, CO=3, Woods, 1975
Euonymus kiautschovicus Loes - F3, P, W, CO=1, Tulsa, 2010

CLEOMACEAE
Gynandropsis gynandra (L.) Briq. - F3, A, F, CO=2, Muskogee, 1939
Tarenaya hassleriana (Chodat) Iltis - F3, A, F, CO=6, LeFlore, 1913

COMMELINACEAE
Commelina communis L. - F2, A, F, CO=35, Muskogee, 1926
Murdannia keisak (Hassk.) Hand.-Maz. - F3W, P, F, CO = 1, McCurtain, 2013

CONVOLVULACEAE
†*Convolvulus arvensis* L. - F2W, P, F, CO=61, Woods, 1913
Ipomoea coccinea L. - F3, A, F, CO=13, Payne, 1915
Ipomoea hederacea Jacq. - F2, A, F, CO=33, Logan, 1905
Ipomoea purpurea (L.) Roth - F3, A, F, CO=25, Cleveland and Murray, 1919
Ipomoea quamoclit L. - F3, A, F, CO=5, Pushmataha, 1932
Ipomoea wrightii Gray - F3, P, F, CO=1, McCurtain, 1950

CUCURBITACEAE
Citrullus lanatus (Thunb.) Matsum. & Nakai var. *lanatus* - F3, A, F, CO=5, Muskogee, 1928
Cucumis melo L. - F3, A, F, CO=3, Cleveland, 1926
Lagenaria siceraria (Molina) Standl. - F3, A, F, CO=1, Cherokee, 1950

CYPERACEAE
Cyperus difformis L. - F1, A, G, CO=1, Payne, 2012
Cyperus esculentus L. - F2W, P, G, CO=42, Woods, 1913
Cyperus iria - F3, A, G, CO=6, McCurtain, 1962
†*Cyperus rotundus* L. - F2W, P, G, CO=16, McCurtain, 1916

DIOSCOREACEAE
Dioscorea oppositifolia L. - F3, P, F, CO=3, Cherokee, 1960

DIPSACACEAE
†*Dipsacus fullonum* L. - F2W, B, F, CO=5, Delaware, 1956
Scabiosa atropurpurea L. - F3, P, F, CO=1, Bryan, 2015

ELAEAGNACEAE
Elaeagnus angustifolia L. - F2W, P, W, CO=17, Cleveland, 1934
†*Elaeagnus pungens* Thunb. - F3W, P, W, CO=4, Oklahoma, 1931
†*Elaeagnus umbellata* Thunb. - F3W, P, W, CO=5, Comanche, 1989

EUPHORBIACEAE
Ricinus communis L. - F3, A, F, CO=6, Unknown, 1930
Triadica sebifera (L.) Small – F2W, P, T, CO=1, McCurtain, 2019

FABACEAE
†*Albizia julibrissin* Durazz. - F2W, P, W, CO=28, Payne, 1946
†*Alhagi maurorum* Medik. - F3, P, W, CO=11, Cotton, 1947
Astragalus chinensis L. f. - F3, P, F, CO=1, Payne, 1940
Arachis hypogaea L. - F3, P, F, CO=2, Caddo, 1944
Erythrostemon gilliesii (Wall. ex Hook.) Klotzsch - F3, P, W, CO=11, Payne, 1941
Colutea arborescens L. - F3, P, W, CO=2, Payne, 1939
Galega officinalis L. - F3, P, F, CO=1, Comanche, 1937
Halimodendron halodendron (L.f.) Voss - F3, P, W, CO=1, Ellis, 1964
Kummerowia stipulacea (Maxim.) Makino - F3, A, F, CO=35, Payne, 1937
Kummerowia striata (Thunb.) Schindl. - F3, A, F, CO=20, Payne, 1937
Lathyrus hirsutus L. - F3, A, F, CO=20, Delaware, 1940
Lathyrus latifolius L. - F3, P, F, CO=11, Pushmataha, 1932
Lathyrus sativus L. - F3, A, F, CO=1, Tulsa, 2003
Lespedeza bicolor Turcz. - F3, P, F, CO=2, Coal, 1989
Lespedeza cuneata (Dum. Cours.) G. Don - F1, P, F, CO=36, Johnston, 1961
Lespedeza thunbergii (DC.) Nakai - F3, P, F, CO=2, Ottawa, 2004
Lotus corniculatus L. - F3, P, F, CO=3, Cleveland, 2003
Medicago arabica (L.) Huds. - F3, A, F, CO=10, Cleveland, 1914
Medicago lupulina L. - F2, P, F, CO=35, Oklahoma, 1925
Medicago minima (L.) L. - F2, A, F, CO=34, Murray, 1929
Medicago orbicularis (L.) Bartal. - F3, A, F, CO=11, Murray, 1948
Medicago polymorpha L. - F3, P, F, CO=8, McCurtain, 1938
Medicago sativa L. - F2, P, F, CO=43, Cleveland, 1919
Melilotus albus Medik. - F2, B, F, CO=23, Woods, 1913
Melilotus indicus (L.) All. - F3, A, F, CO=1, Noble, 1939
Melilotus officinalis (L.) Lam. - F2, A, F, CO=60, Cleveland, 1919
Pisum sativum L. - F3, A, F, CO=6, LeFlore, 1944
†*Pueraria montana* (Lour.) Merr. - F2W, P, V, CO=15, Payne, 1941

Securigera varia (L.) Lassen - F3, P, F, CO=17, Payne, 1938
Senna occidentalis (L.) Link - F3, P, F, CO=7, LeFlore, 1913
Trifolium arvense L. - F2, A, F, CO=24, Haskell, 1948
Trifolium campestre Schreb. - F2, B, F, CO=44, Cleveland, 1926
Trifolium dubium Sibth. - F2, A, F, CO=29, Cleveland, 1927
Trifolium hybridum L. - F3, A, F, CO=9, Cleveland, 1927
Trifolium incarnatum L. - F2, A, F, CO=29, Kay, 1935
Trifolium pratense L. - F3, P, F, CO=26, Caddo, 1913
Trifolium repens L. - F2, P, F, CO=34, Caddo, 1913
Trifolium resupinatum L. - F3, A, F, CO=11, McCurtain, 1950
Trifolium striatum L. - F3, A, F, CO=1, Choctaw, 1939
Trifolium subterraneum L. - F3, A, F, CO=1, LeFlore, 1937
Trifolium vesiculosum Savi – F3, A, F, CO=20, Johnston, 1973
Vicia cracca L. - F3, P, F, CO=5, Muskogee, 1909
Vicia sativa L. - F2, A, F, CO=36, McClain, 1930
Vicia tetrasperma (L.) Schreb. - F3, A, F, CO=1, Murray, 1942
Vicia villosa Roth - F2, B, F, CO=35, Cleveland, 1903
Wisteria floribunda (Willd.) DC. – F3, P, V, CO=1, McCurtain, 2010

GERANIACEAE
Erodium cicutarium (L.) L'Hér. ex Aiton - F2, A, F, CO=40, Oklahoma, 1923
Geranium dissectum L. - F3, A, F, CO=10, Bryan, 1997
Geranium molle L. - F3, B, F, CO=7, Cherokee, 1947
Geranium pusillum L. - F3, B, F, CO=24, Cherokee, 1955

HELIOTROPIACEAE
Heliotropium indicum L. - F2, A, F, CO=30, McCurtain, 1916

HALORAGACEAE
Myriophyllum aquaticum (Vell.) Verdc. - F2W, P, F, CO=14, Carter, 1936
Myriophyllum spicatum L. - F2W, P, F, CO=10, Comanche, 1959

HYDROCHARITACEAE
Egeria densa Planch. - F3W, P, F, CO=7, Payne, 1940
**Hydrilla verticillata* (L. f.) Royle - F2W, P, F, CO=3, Murray, 2006

HYDRANGEACEAE
Philadelphus inodorus L. - F3, P, W, CO=4, Payne, 1933

HYPERICACEAE
Hypericum perforatum L. - F2, P, W, CO=25, Muskogee, 1951

IRIDACEAE
Iris domestica (L.) Goldblatt & Mabb. - F3, P, F, CO=5, McCurtain, 1930
Iris germanica L. – F3, P, F, CO=2, Comanche, 1995
Iris pseudacorus L. - F3, P, F, CO=2, McCurtain, 2002

JUNCACEAE
Juncus capitatus Weigel - F3, P, G, CO=3, McCurtain, 1980

LAMIACEAE
Ajuga reptans L. - F3, P, F, CO=2, Bryan, 1973
Galeopsis tetrahit L. - F3, A, F, CO=1, LeFlore, 1969
Glechoma hederacea L. - F3, P, F, CO=14, Payne, 1936
Lamium amplexicaule L. - F2, B, F, CO=67, Cleveland, 1916
Lamium purpureum L. - F2, A, F, CO=40, Cherokee, 1925
Leonurus cardiaca L. - F3, P, F, CO=3, Cherokee, 1925
Leonurus sibiricus L. - F3, P, F, CO=3, Cherokee, 1956
Marrubium vulgare L. - F2, P, F, CO=25, Pawnee, 1905
Melissa officinalis L. - F3, P, F, CO=4, Mayes, 1955
Mentha × *gracilis* Sole (pro sp.) [*arvensis* × *spicata*] - F3, P, F, CO=2, Washington, 1972
Mentha arvensis L. - F3, P, F, CO=2, Oklahoma, 1940
Mentha spicata L. - F2, P, F, CO=11, Cotton, 1934
Mentha x *piperita* (pro sp.) - F2, P, F, CO=12, Cleveland, 1924
Nepeta cataria L. - F3, P, F, CO=10, Cherokee, 1924
†*Perilla frutescens* (L.) Britton - F2, A, F, CO=20, Muskogee, 1927
Vitex agnus-castus L. - F3, P, F, CO=8, Pawnee, 1935

LILIACEAE
Ornithogalum umbellatum L. - F3, P, F, CO=12, Kay, 1945

LINACEAE
Linum usitatissimum L. - F3, A, F, CO=6, Carter, 1913

LYGODIACEAE
†*Lygodium japonicum* (Thunb.) Sw. - F3, P, F, CO=1, McCurtain, 1980

LYTHRACEAE
Lagerstroemia indica L. - F3, P, W, CO=6, LeFlore, 1988
*†*Lythrum salicaria* L. - F3, P, F, CO=4, Cleveland and Oklahoma, 1993

MALVACEAE
Abutilon theophrasti Medik. - F2, A, F, CO=30, Osage, 1913
Alcea rosea L. - F3, P, F, CO=3, Pottawatomie, 1934
Hibiscus trionum L. - F3, A, F, CO=20, Stephens, 1905
Malva neglecta Wallr. - F2, P, F, CO=19, Oklahoma, 1925
Sida abutifolia Mill. - F3, P, F, CO=11, Murray, 1940

MARSILIACEAE
**Marsilea mutica* Mett. – F3W, P, F, CO=1, Hughes, 2001

MELIACEAE
†*Melia azedarach* L. - F2W, P, W, CO=8, McCurtain, 1944

MENYANTHACEAE
Nymphoides peltata (S.G. Gmel.) Kuntze - F3, P, F, CO=2, Bryan, 1947

MOLLUGINACEAE
Glinus lotoides L. - F3, A, F, CO=15, Unknown, 1894

MORACEAE
†*Broussonetia papyrifera* (L.) L'Hér. ex Vent. - F3W, P, W, CO=11, Tulsa, 1931
Fatoua villosa (Thunb.) Nakai - F3, A, F, CO=10, Grady, 1985
Morus alba L. - F2, P, W, CO=51, Cleveland, 1926

NYCTAGINACEAE
Mirabilis jalapa L. - F3, P, F, CO=6, Cherokee, 1952

OLEACEAE
Jasminum nudiflorum Lindl. – F3, P, W, CO=2, Bryan,1993
Ligustrum quihoui Carr. - F3, P, W, CO=3, Oklahoma, 1959
Ligustrum sinense Lour. - F1, P, W, CO=22, Muskogee, 1940
Ligustrum vulgare L. - F2W, P, W, CO=7, Bryan, 1972

ONAGRACEAE
Ludwigia grandiflora (Michx.) Greuter & Burdet - F3, P, F, CO=6, Payne, 1946

PAPAVERACEAE
†*Glaucium corniculatum* (L.) J.H. Rudolph - F3, A, F, CO=3, Payne, 1993
Glaucium flavum Crantz - F3, B, F, CO=2, Kiowa and Tillman, 1985
Papaver dubium L. - F3, A, F, CO=6, Muskogee, 1939

PAULOWNIACEAE
†*Paulownia tomentosa* (Thunb.) Siebold & Zucc. ex Steud. - F3, P, W, CO=2, Comanche, 1946

PHYLLANTHACEAE
Phyllanthus urinaria L. - F3, A, F, CO=1, Grady, 1999

PLANTAGINACEAE
Plantago lanceolata L. - F2, P, F, CO=25, Cleveland, 1907
Plantago major L. - F2, P, F, CO=29, Oklahoma, 1931

POACEAE
Aegilops cylindrica Host - F2, A, G, CO=50, Payne, 1938
Agrostis gigantea Roth -F3, P, G, CO=11, Caddo, 1913
Agrostis stolonifera L. - F3, P, G, CO=7, Caddo, 1913
Aira caryophyllea L. - F2, A, G, CO=26, Muskogee, 1939
Aira elegantissima Schur - F3, A, G, CO=19, McCurtain, 1949
Anthoxanthum aristatum Boiss. - F3, A, G, CO=2, McIntosh, 2009
Anthoxanthum odoratum L. - F3, A, G, CO=4, Choctaw, 2001
Arthraxon hispidus (Thunb.) Makino - F3, P, G, CO=4, Cherokee, 1953
†*Arundo donax* L. - F2W, P, G, CO=10, Garfield, 1967
Avena fatua L. - F2, A, G, CO=23, Muskogee, 1927
†*Bothriochloa bladhii* (Retz.) S.T. Blake - F3W, P, G, CO=3, Woods, 1969
Bothriochloa ischaemum (L.) Keng - F1, P, G, CO=39, Payne, 1940
Briza minor L. - F3, A, G, CO=8, McCurtain, 1973
Bromus arvensis L. - F1, A, G, CO=65, Cleveland, 1923
Bromus commutatus Schrad. - F3, A, G, CO=32, Muskogee, 1927
Bromus catharticus Vahl - F2, P, G, CO=63, Love, 1913
Bromus diandrus Roth - F3, A, G, CO=3, Payne, 1940
Bromus hordeaceus L. - F2, A, G, CO=21, Muskogee, 1955

Bromus inermis Leyss. - F3, P, G, CO=9, Payne, 1924
Bromus racemosus L. - F3, A, G, CO=5, Cleveland, 1923
Bromus secalinus L. - F2, A, G, CO=35, Unknown, 1905
Bromus sterilis L. - F3, A, G, CO=5, Rogers, 1957
Bromus tectorum L. - F1, A, G, CO=66, Oklahoma, 1925
Chloris gayana Kunth - F3, P, G, CO=2, Payne, 1962
Cynodon dactylon (L.) Pers. - F1, P, G, CO=45, Oklahoma, 1924
Cynosurus echinatus L. - F3, A, G, CO=5, Carter, 1947
Dactylis glomerata L. - F2, P, G, CO=17, Payne, 1922
Catapodium rigidum (L.) Dony - F3, A, G, CO=1, Murray, 2012
Digitaria ciliaris (Retz.) Koeler - F2, A, G, CO=29, Ottawa, 1913
Digitaria ischaemum (Schreb.) Muhl. - F2, A, G, CO= 21, Muskogee, 1927
Digitaria sanguinalis (L.) Scop. – F2, A, G, CO=69, Washita, 1913
Digitaria violascens Link - F3, P, G, CO=5, McCurtain, 1950
Echinochloa colona (L.) Link - F3, A, G, CO=17, LeFlore, 1938
Echinochloa crus-galli (L.) Beauv. - F2, A, G, CO=72, Blaine, 1913
Echinochloa crus-pavonis (Kunth) J.A. Schultes - F3, A, G, CO=3, Cotton, 1940
Echinochloa muricata (Beauv.) Fern. - F3, A, G, CO=31, Blaine, 1913
Eleusine indica (L.) Gaertn. - F2, A, G, CO=48, Major, 1913
Elymus repens (L.) Gould - F3, P, G, CO=1, Greer, 1931
Eragrostis barrelieri Daveau - F2, A, G, CO=35, Grady, 1938
Eragrostis cilianensis (All.) Vign. ex Janchen - F2, A, G, CO=57, Harmon, 1913
Eragrostis curvula (Schrad.) Nees - F2W, P, G, CO=28, Payne, 1941
Eragrostis japonica (Thunb.) Trin. - F3, A, G, CO=6, Coal, 1949
Eragrostis lehmanniana Nees - F3, P, G, CO=3, Payne, 1940
Eragrostis minor Host - F3, A, G, CO=3, Pontotoc, 1952
Eragrostis pilosa (L.) P. Beauv. - F3, A, G, CO= 36, Logan, 1914
Eragrostis superba Peyr. - F3, P, G, CO=1, Woods, 1992
Glyceria declinata Bréb. - F3, P, G, CO=1, Love, 2018
Holcus lanatus L. - F3, P, G, CO=3, Delaware, 1962
Hordeum murinum L. - F3, A, G, CO=2, Cleveland, 1938
Hordeum vulgare L. - F3, A, G, CO=10, Payne, 1940
Lolium perenne L. - F2W, P, G, CO=41, Cleveland, 1923
Lolium temulentum L. - F3, A, G, CO=4, Payne, 1917
†*Microstegium vimineum* (Trin.) A. Camus - F2W, A, G, CO=3, Cherokee, 2004
Oryza sativa L. - F3, A, G, CO=1, McCurtain, 1974
Panicum antidotale Retz. - F3, P, G, CO=1, Kiowa, 1964
Panicum miliaceum L. - F3, A, G, CO=2, McCurtain, 1930
Paspalum dilatatum Poir. - F2, P, G, CO=41, Harmon, 1913
Paspalum notatum Alain ex Flüggé - F2, P, G, CO=7, Pushmataha, 1968
Paspalum urvillei Steud. - F3, P, G, CO=5, McCurtain, 1936
Pennisetum glaucum (L.) R. Br. - F2, P, G, CO=48, Kay, 1913
Phalaris canariensis L. - F3, A, G, CO=6, Payne, 1922
Phleum pratense L. - F3, P, G, CO=2, Johnston, 1986
Poa annua L. - F2, A, G, CO=69, Carter, 1913
Poa bulbosa L. - F3, P, G, CO=8, Pontotoc, 1947
Poa compressa L. - F3, P, G, CO=10, Caddo, 1913
Poa pratensis L. – F2, P, G, CO=37, Garvin, 1913
Polypogon monspeliensis (L.) Desf. - F2, A, G, CO=34, Cleveland, 1922
Polypogon viridis (Gouan) Breistr. - F1, P, G, CO=2, Cimarron, 1947
†*Saccharum ravennae* (L.) L. - F2W, P, G, CO=17, McCurtain, 1930

Schedonorus phoenix (Scop.) Holub - F1, P, G, CO=30, Bryan, 1963
Schedonorus pratensis (Huds.) P. Beauv. - F3, P, G, CO=3, Osage, 2005
Sclerochloa dura (L.) Beauv. - F3, A, G, CO=9, Cleveland, 1973
Secale cereale L. - F3, A, G, CO=10, Marshall, 1957
Setaria faberi Herrm. - F3, A, G, CO=1, Craig, 1999
Setaria italica (L.) Beauv. - F3, A, G, CO=13, Woods, 1913
Setaria pumila (Poir.) Roem. & Schult. - F2, A, G, CO=18, Grady, 1972
Setaria verticillata (L.) P. Beauv. - F3, A, G, CO=2, Muskogee, 1939
Setaria viridis (L.) Beauv. - F2, A, G, CO=55, Woods, 1913
Sorghum bicolor (L.) Moench - F3, A, G, CO=9, Muskogee, 1927
Sorghum halepense (L.) Pers. - F1, P, G, CO=64, Harmon, 1913
Stenotaphrum secundatum (Walter) Kuntze - F3, P, G, CO=2, Carter, 1944
Thinopyrum elongatum (Host) D.R. Dewey – F3, P, G, CO=3, Payne, 1941
Thinopyrum ponticum (Podp.) Barkworth & D.R. Dewey - F3, P, G, CO=2, Grant, 1999
Tripidium ravennae (L.) H. Scholz - F1, P, G, CO= 17, McCurtain, 1930
Triticum aestivum L. - F3, A, G, CO=19, Muskogee, 1927
Vulpia myuros (L.) C.C. Gmel. - F3, A, G, CO=12, Adair, 1950

POLYGONACEAE
Fagopyrum esculentum Moench - F3, A, F, CO=1, Cherokee, 2004
Fallopia convolvulus (L.) Á. Löve - F2, A, F, CO=27, Woods, 1913
Fallopia japonica (Houtt.) Ronse Decr. var. *japonica* - F3, P, F, CO=2, Cleveland, 1936
Polygonum aviculare L. - F2, P, F, CO=54, Major, 1913
Polygonum aviculare ssp. *buxiforme* (Small) Costea & Tardif – F2, P, F, CO=3, Cherokee, 1957
Persicaria hydropiper (L.) Opiz - F3, A, F, CO=24, Kay, 1913
Persicaria longiseta (Bruijn) Kitag – F3, A, F, CO=5, McCurtain, 1994
Persicaria orientalis (L.) Spach - F3, A, F, CO=3, Pushmataha, 1932
Persicaria maculosa Gray - F2, A, F, CO=46, Kiowa (Swanson), 1913
Persicaria posumbu (Buch.-Ham. ex D. Don) H. Gross - F3, A, F, CO=1, Okmulgee, 2013
Rumex acetosella L. - F3, P, F, CO=19, Alfalfa, 1919
Rumex conglomeratus Murr. - F3, P, F, CO=1, McCurtain, 1956
Rumex crispus L. - F2, P, F, CO=65, Cleveland, 1903
Rumex obtusifolius L. - F3, P, F, CO=14, Ottawa, 1913
Rumex patientia L. - F3, P, F, CO=4, Beaver, 1913
Rumex pulcher L. - F3, P, F, CO=16, McCurtain, 1930

PONTEDERIACEAE
†*Eichhornia crassipes* (Mart.) Solms - F2W, P, F, CO=2, Payne, 1931

PORTULACACEAE
Portulaca halimoides L. – F3, A, F, CO=5, Cimarron, 1936
Portulaca oleracea L. – F3, A, F, CO=31, Woods, 1913

POTAMOGETONACEAE
Potamogeton crispus L. - F2, P, F, CO=8, Cleveland, 1937

PRIMULACEAE
Anagallis arvensis L. - F3, A, F, CO=6, Delaware, 1961
Anagallis foemina Mill. – F3, A, F, CO=1, Cleveland, 1966
Anagallis minima (L.) E.H.L. Krause - F3, A, F, CO=12, Muskogee, 1927

RANUNCULACEAE
Clematis terniflora DC. - F2, P, F, CO=18, Muskogee, 1940
Consolida ajacis (L.) Schur - F3, A, F, CO=19, Cleveland, 1927
Ranunculus muricatus L. - F3, A, F, CO=1, McIntosh, 2001
Ranunculus parviflorus L. - F3, A, F, CO=9, McCurtain, 1938
Ranunculus sardous Crantz - F3, A, F, CO=3, Sequoyah, 1955
Ranunculus testiculatus Crantz - F3, A, F, CO=1, Cimarron, 2014

ROSACEAE
Aphanes microcarpa (Boiss. & Reut.) Rothm. - F3, A, F, CO=1, McCurtain, 1984
Duchesnea indica (Andr.) Focke - F3, P, F, CO=7, McCurtain, 1948
†*Potentilla recta* L. - F2W, P, F, CO=38, Cherokee, 1924
Prunus mahleb L. - F3, P, W, CO=2, Pottawatomie, 1967
Prunus persica (L.) Batsch - F3, P, W, CO=19, Muskogee, 1929
†*Pyrus calleryana* Decne. - F3W, P, W, CO=6, Cherokee, 2004
Rosa multiflora Thunb. - F2, P, W, CO=37, Delaware, 1956
Rubus bifrons Vest ex Tratt. - F3, P, W, CO=11, Payne, 1946

RUBIACEAE
Cruciata pedemontana (Bellardi) Ehrend. - F3, A, F, CO=15, McCurtain, 1970
Galium aparine L. - F2, A, F, CO=65, Cimarron, 1913
Galium tricornutum Dandy - F3, A, F, CO=1, Hughes, 2006
Sherardia arvensis L. - F3, A, F, CO=35, LeFlore, 1947

RUTACEAE
Poncirus trifoliata (L.) Raf. - F3, P, W, CO=6, Bryan, 1962

SALICACEAE
Populus alba L. - F3, P, W, CO=11, Pottawatomie, 1932

SAPINDACEAE
Cardiospermum halicacabum L. - F2, B, F, CO=35, Unknown (Little River), 1903

SCROPHULARIACEAE
Chaenorhinum minus (L.) Lange - F3, A, F, CO=3, Tulsa, 1975
Kickxia elatine (L.) Dumort. - F3, A, F, CO=6, Delaware, 1938
†*Linaria dalmatica* (L.) Mill. - F3, P, F, CO=3, Texas, 1971
Linaria vulgaris Mill. - F3, P, F, CO=13, Cleveland, 1928
Mazus japonicus (Thunb.) Kuntze - F3, A, F, CO=6, Cherokee, 1952
Parentucellia viscosa (L.) Caruel - F3, A, F, CO=1, McCurtain, 2006
Verbascum blattaria L. - F3, B, F, CO=21, Osage, 1913
Verbascum thapsus L. - F2, B, F, CO=38, LeFlore, 1913
Veronica agrestis L. - F3, A, F, CO=5, Payne, 1934
Veronica arvensis L. - F2, A, F, CO=51, Oklahoma, 1920
Veronica hederifolia L. - F3, A, F, CO=4, Tulsa, 1957
Veronica persica Poir. - F3, A, F, CO=10, Delaware, 1961
Veronica polita Fr. - F3, A, F, CO=27, Payne, 1940
Veronica triphyllos L. - F3, A, F, CO=2, Cleveland, 1964

SIMAROUBACEAE
†*Ailanthus altissima* (Mill.) Swingle - F2W, P, F, CO=27, Cleveland, 1932

SOLANACEAE
Datura inoxia P. Mill. - F3, P, F, CO=23, Cherokee, 1951
Datura stramonium L. - F2, A, F, CO=39, Kay, 1913
Lycium barbarum L. - F3, P, V, CO=13, LeFlore, 1914
Nicandra physalodes (L.) Gaertn. - F3, A, F, CO=1, Grady, 2003
Physalis philadelphica Lam. var. *immaculata* Waterf. - F3, A, F, CO=1, Unknown, 1956
Solanum lycopersicum L. - F3, A, F, CO=2, McCurtain, 1976
Solanum physalifolium Rusby - F3, A, F, CO=10, Sequoyah, 1954

SPHENOCLEACEAE
Sphenoclea zeylanica Gaertn. - F3, A, F, CO=1, McCurtain, 1983

TAMARICACEAE
Tamarix chinensis Lour. - F1, P, W, CO=23, Texas, 1946
Tamarix gallica L. - F1, P, W, CO=49, Oklahoma, 1910
Tamarix parviflora DC. - F1, P, W, CO=15, Cleveland, 1930
Tamarix ramosissima Ledeb. - F1, P, W, CO=44, Cleveland, 1921

URTICACEAE
Urtica urens L. – F3, A, F, CO=2, Okmulgee, 2013

ULMACEAE
Ulmus parvifolia Jacq. - F3, P, W, CO=13, Payne, 1946
Ulmus pumila L. - F1, P, W, CO=33, Cleveland, 1934

VERBENACEAE
Verbena bonariensis L. - F2, B, F, CO=4, McCurtain, 1947
Verbena brasiliensis Vell. - F3, A, F, CO=5, Johnston, 1967

VIOLACEAE
Viola tricolor L. - F3, A, F, CO=11, Oklahoma, 1925

XANTHORRHOEACEAE
Hemerocallis fulva (L.) L. - F3, P, F, CO=2, LeFlore, 1949
Hemerocallis lilioasphodelus L. - F3, P, F, CO=5, Cherokee, 1959
Ornithogalum umbellatum L. - F3, P, F, CO=13, Kay, 1945

ZYGOPHYLLACEAE
Tribulus terrestris L. - F2, A, F, CO=57, Greer, 1912

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GRINDELIA (ASTERACEAE) IN NUEVO LEÓN, MEXICO: TAXONOMIC CLARIFICATIONS

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ABSTRACT

Numerous recent collections in Nuevo León, Mexico, make it possible to clarify definitions and geographic distributions for species of *Grindelia*, including *G. greenmanii*, *G. hintoniorum*, *G. turneri*, and *G. villarrealii*. Typical *G. inuloides* does not occur in Nuevo León. Collections are cited and mapped and illustrations of representative collections are provided.

In an earlier review of the taxonomy of *Grindelia* from Texas and Mexico (Nesom 1990, 1992), I described four new species from Nuevo León — *G. turneri*, *G. hintoniorum*, *G. villarreallii*, and *G. vetimontis* — in addition to recognizing the presence of similar species, *G. greenmanii* Steyerm. and the more widespread *G. inuloides* Willd. Accumulation of additional collections in the nearly 30 intervening years makes it possible to clarify species morphological boundaries and geographical patterns.

Grindelia greenmanii is a distinctive species, but it has a slightly narrower range than recognized in 1990. *Grindelia vetimontis* is similar to *G. greenmanii* and the two perhaps have a sister relationship. Typical *G. inuloides* does not occur in Nuevo León; collections earlier identified as *G. inuloides* are recognized here mostly as *G. hintoniorum* and *G. villarreallii*. *Grindelia villarrealii* is a distinctive species of the Peña Nevada area, where it co-occurs only with *G. obovatifolia* Blake. Detailed comments are provided below.

GRINDELIA GREENMANII Steyerm., Ann. Missouri Bot. Garden 21: 460. 1934. **TYPE**: **MEXICO**. **Coahuila**. [Mpio. Arteaga:] "Lerios" [Los Lirios], 10-13 Jul 1880, *E. Palmer 471* (holotype: GH!; isotypes: K image, NY image, PH!, US!, YU image). The PH sheet has the original label by Palmer, noting the collection data as "July 10 to 13."

Grindelia greenmanii is characterized by its thick rhizomes, villous to sparsely pilose stems, stipitate-glandular vestiture (stems, leaves, involucres), and peduncles with only slightly reduced leaves extending to immediately below the heads as foliaceous bracts. The apices of foliar teeth are variable — acute and usually neither glandular nor spinulose, but sometimes with a short-indurate point, or sometimes indurate or slightly glandular — variable even on a single plant. Plants of *G. greenmanii* in the Arteaga area of Coahuila tend to have smaller involucres and smaller basal leaves than those in the Cerro Potosí area.

Flowering (Jun–)Jul–Oct(–Nov); alpine and subalpine and meadows, spruce, pine, and pine-oak woods, (1600–)2200–3650 m. *Grindelia greenmanii* is primarily a high-elevation species but plants occur lower in pine-oak areas immediately around high-elevation areas where the species is common. The lowest locality is is the Cañón La Boca, between Cola de Caballo and Laguna Sánchez, at 1600 m (*Villarreal 2836*, MEXU). The species is restricted to two relatively discrete, disjunct regions: (1) the Arteaga region of Coahuila and (2) Cerro Potosí and the immediately surrounding area (Fig. 1).

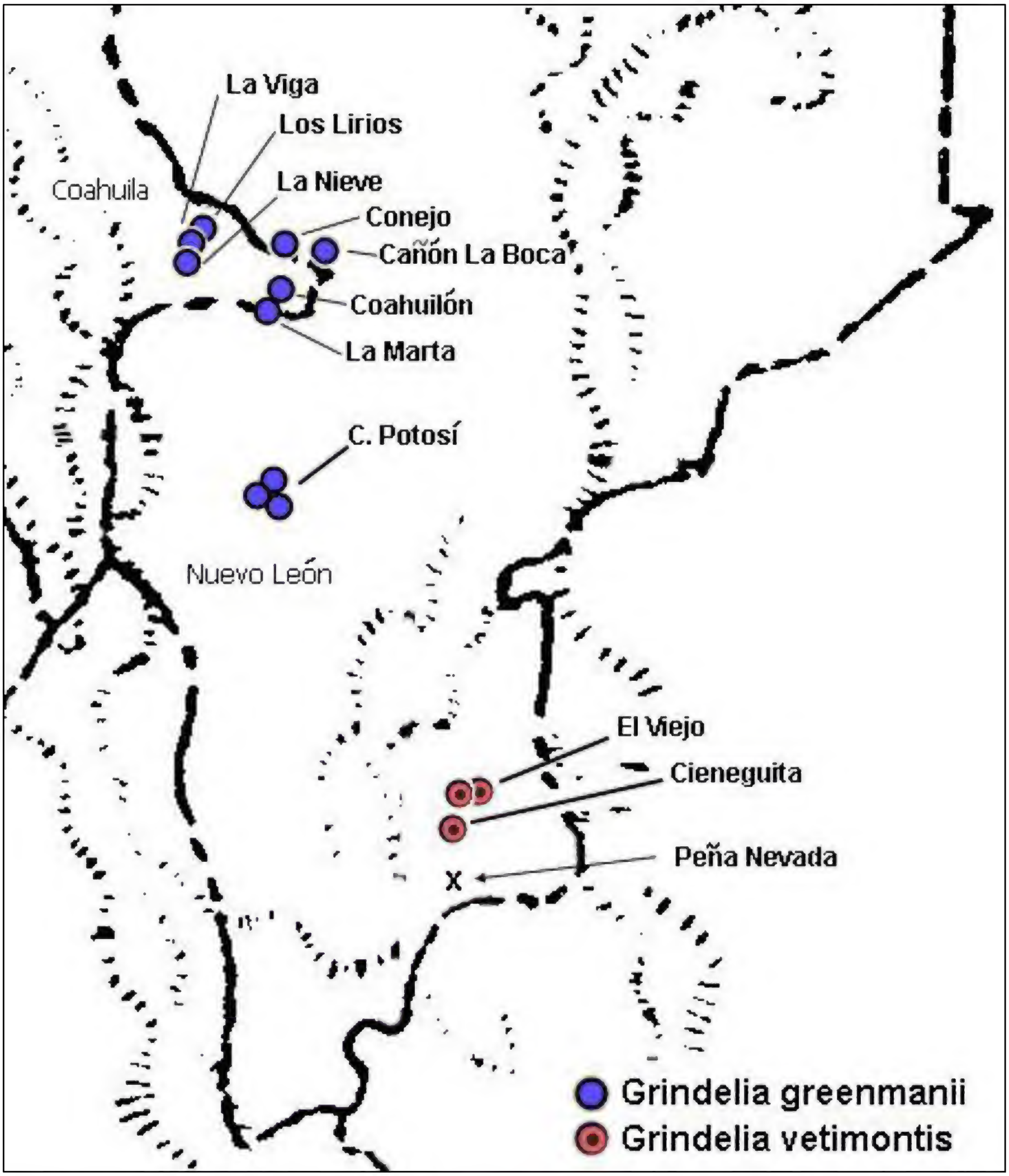

Figure 1. Distribution of ***Grindelia greenmanii*** (Sierra La Viga, Sierra de Los Lirios, Sierra La Nieve, Puerto Conejo, Cañón La Boca, Sierra El Coahuilón, Sierra La Marta, and Cerro Potosí and immediate vicinity) and ***G. vetimontis*** (Cerro El Viejo and slightly to the southwest, between Cieneguita and San Josecito). Collections in the area of Cerro Peña Nevada (Picacho San Onofre) previously identified as *G. greenmanii* and *G. inuloides* are here referred to *G. villarrealii* (see Fig. 15, text and specimen citations).

Figure 2. *Grindelia greenmanii*, Mpio. Galeana, Cerro Potosí, *Hinton 17148* (GBH).

Figure 3. *Grindelia greenmanii*, Mpio. Arteaga, Sierra La Marta, *Hinton 17890* (GBH).

Figure 4. *Grindelia greenmanii*, Mpio. Arteaga, El Paso, *Hinton 24382* (GBH).

Figure 5. *Grindelia greenmanii*, Mpio. Arteaga, Los Lirios to El Cercado, *Hinton 25428* (GBH).

Figure 6. *Grindelia greenmanii*. Mpio. Arteaga, Jamé to Rayones, *Hinton 27785* (GBH).

GRINDELIA VETIMONTIS Nesom, Phytologia 68: 330. 1990. **TYPE**: **MEXICO**. **Nuevo León**. [Mpio. Gral. Zaragoza:] Cerro del Viejo, 15 mi W of Dulces Nombres, rocky slopes in open pine forest, 3330 m, 18 Aug 1948, *F.G. Meyer & D.J. Rogers 2988* (holotype: MO!; isotype: F!).

Additional collections. **Nuevo León**. Mpio. Zaragoza: Cerro El Viejo, oak and pine woods, 3310 m, 5 Oct 1992, *Hinton et al. 22398* (GBH, MEXU); Cerro El Viejo, pine woods, 3125 m, 6 Oct 1992, *Hinton et al. 22434* (GBH); San Jose to La Cieneguita, oak woods, 2270 m, 3 Oct 1998, *Hinton et al. 27274* (GBH).

Grindelia vetimontis was described as differing from *G. greenmanii* in eglandular stems, leaves with rounded apices, and phyllaries nervate in the basal, white-indurate portion. Leaf teeth have acute, non-indurate apices. Diagnostic features are detailed in the couplet below (and compare Figs. 2-6 with Figs. 7-11).

1. Stems villous, eglandular; medial cauline leaves mostly oblong, apices rounded to obtuse; phyllaries distinctly nervate in the indurate proximal portion, green distal portion triangular to narrowly oblong-lanceolate, sometimes loose but not recurving ..... **Grindelia vetimontis**

1. Stems villous and stipitate-glandular; cauline leaves mostly lanceolate-triangular, apices acute to acute-acuminate; phyllaries enervate or indistinctly nervate in the indurate proximal portion, green distal portion linear-triangular to nearly linear-terete, often recurving ..... **Grindelia greenmanii**

The two taxa are similar in their rhizomatous habit and non-punctate leaves, the basal large and usually persistent, the cauline continuing distally little reduced in size, subtending the involucres as foliaceous bracts. Bartoli and Tortosa (2012) treated *G. vetimontis* as a synonym of *G. greenmanii*, noting that they observed intermediates in the Peña Nevada area (i.e., *Nesom 4800* and *Breedlove 63552*; without specifying the nature of the putative intermediacy) — both of these collections are taprooted, without foliaceous involucral bracts, and identified here as *G. hintoniorum*.

Many taxa in various genera mirror the distribution pattern of *Grindelia greenmanii* (Fig. 1), divided between high elevation habitats of Cerro Potosí and the "Arteaga" mountains (McDonald 1993). McDonald also described a common disjunction pattern between Arteaga/Cerro Potosí and Peña Nevada, often between closely similar species that appear to be evolutionary vicariads. The latter probably is the case in *G. greenmanii* and *G. vetimontis*.

Figure 7. *Grindelia vetimontis*, F isotype (see Fig. 8), detail.

Figure 8. *Grindelia vetimontis*, Mpio. Gral. Zaragoza, Cerro El Viejo, F isotype.

Figure 9. *Grindelia vetimontis*, Mpio. Gral. Zaragoza, Cerro El Viejo, *Hinton 22398* (GBH)

Figure 10. *Grindelia vetimontis*, Mpio. Gral. Zaragoza, Cerro El Viejo, *Hinton 22434* (GBH)

Figure 11. *Grindelia vetimontis*, Mpio. Gral. Zaragoza, between San Josecito and Cieneguita, *Hinton 27274* (GBH).

Grindelia obovatifolia Blake also occurs in the area of Cerro El Viejo (e.g., *Nesom 7718*–MEXU, TEX) and is similar to *G. vetimontis* in its rhizomatous habit and non-punctate, clasping leaves with rounded apices, but it differs in sparse cauline vestiture, reduced distal cauline leaves, smaller heads, strongly graduated phyllaries with abruptly acuminate-linear, recurving/recoiling apices, and achenes (at maturity) with distinct transverse furrows. See Figs. 12 and 13. Rarely confused with any other species.

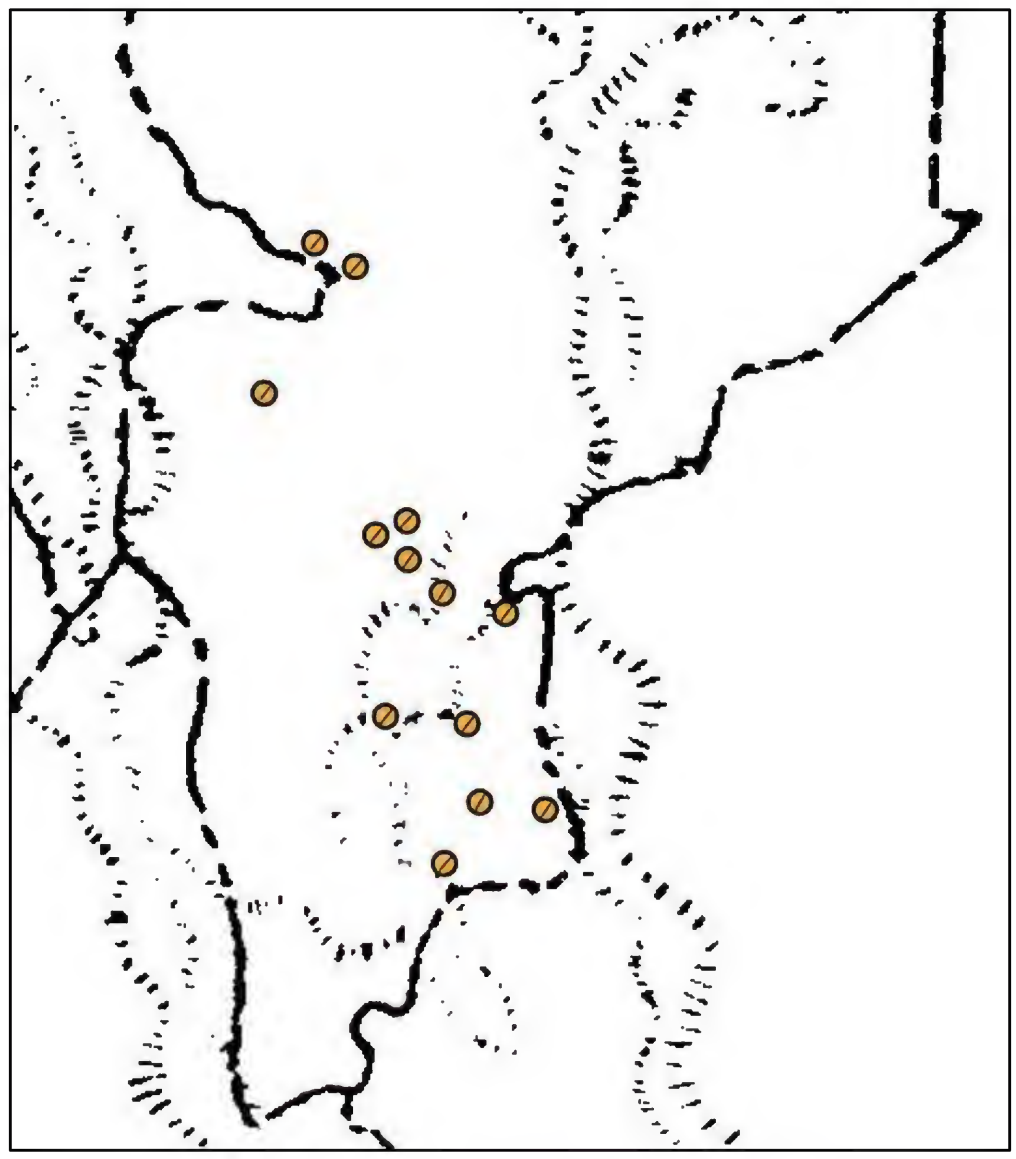

Figure 12. Distribution of *Grindelia obovatifolia*.

Figure 13. *Grindelia obovatifolia*, involucral bracts. Mpio. Iturbide, *Hinton et al. 21231* (GBH).

Figure 14. *Grindelia obovatifolia*. Mpio. Galeana, *Hinton 21316* (GBH).

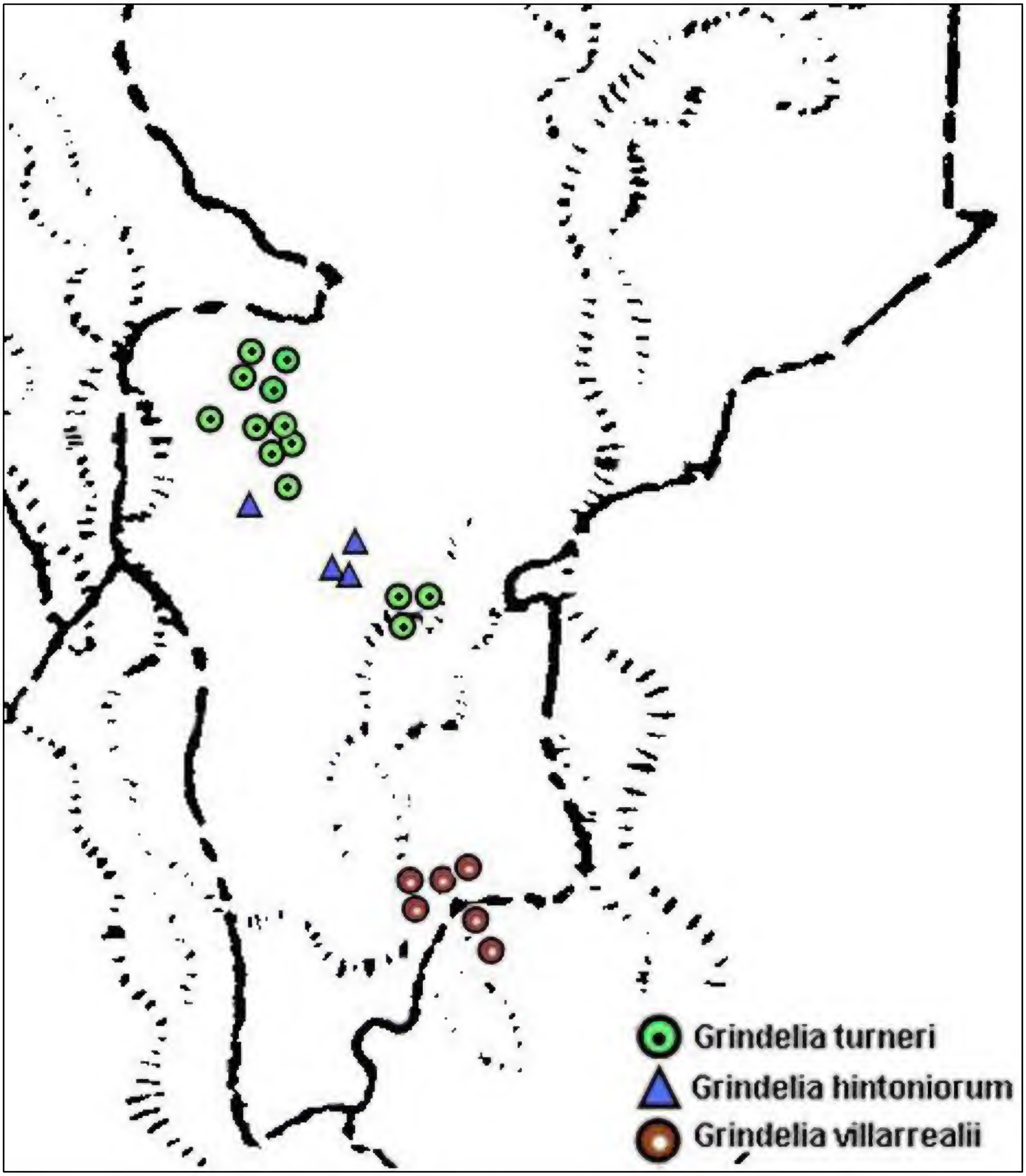

Figure 15. Distribution of *Grindelia turneri*, *G. hintoniorum*, and *G. villarrealii*.

GRINDELIA TURNERI Nesom, Phytologia 68: 313. 1990. **TYPE**: **MEXICO**. **Nuevo León**. Mpio. Galeana: Between San Pablo and Tanquecillos, 0.5 mi S of San Pablo, on the road between San Rafael Jct and Galeana, fallow fields in valley, area of pines on high slopes of valley margins, 2320 m, 27 Aug 1989, *G.L. Nesom 7189* (holotype: TEX; isotypes: ANSM, COLO, ENCB, F, GH, KANU, MEXU, MO, NY, RM, US, WAT, WIS).

Flowering (May–)Jul–Oct(–Nov). Oak and oak-pine areas, meadows in pine woods, grassy slopes, edge of cultivated fields, roadsides and disturbed sites; 1450–2600 m.

Grindelia turneri is characterized by a perennial, taprooted habit, relatively short, few-branched stems, leaves with blunt, gland-tipped teeth, and pappus awns 2, as long or longer than the disc corollas. Mature achenes "wrinkled" with short, shallow, transverse furrows.

Additional collections. **MEXICO**. **Nuevo León**. Mpio. Galeana: Along gravel road to 18 de Marzo, 8.7 mi E of the jct of the gravel road and Mex Hwy 57, open pine forest, locally common in disturbed habitats along road, rocky loamy soil, probably on gypsum, 5 Aug 1983, *Freeman & Wetter 2056* (MEXU, TEX, WIS-2 sheets); along the road from San Rafael to Derecho de Marzo and Galeana, ca. 8 mi E of San Rafael, 4.4 mi E of La Boca, 6200 ft, 22 Oct 1982, *Grimes 2278* (MEXU, TEX); Tanquecillos, field, 2430 m, 11 May 1980, *Hinton et al. 17760* (GBH); Rancho Aguililla, orchard, 1850 m, 3 Jul 1989, *Hinton et al. 19481* (GBH, MEXU); below Agua Blanca, oak woods, 2270 m, 4 Jul 1992, *Hinton et al. 22268* (GBH); Socorro to San Pablo, meadow, 2355 m, 25 Jul 1995, *Hinton et al. 25402* (GBH, MEXU); San Pablo to San Pedro Sotolar, edge of cultivated field, 2425 m, 11 Jul 1998, *Hinton et al. 27192* (GBH); La Boca to San Pablo, meadow in pine woods, 2420 m, 1 Aug 2001, *Hinton et al. 27681* (GBH); San Pedro Sotolar to San Pablo, roadside meadow in pine woods, 2621 m, 22 May 2005, *Hinton et al. 28344* (GBH); E of San Rafael, 5.6 mi ESE of San Pablo, 30 Nov 1986, *Nesom 5281* (MEXU, TEX); ca. 2 mi W of San Pablo, overlooking the town, open, grassy slopes at edge of pine woods, 2300 m, 27 Aug 1980, *Nesom 7184* (ANSM, KANY, MEXU, MO, NY, RM, TEX, WIS); ca. 2 mi S of Tanquecillos, on road between San Rafael Jct and Galeana, open area of shaly limestone with scattered pines, pine woods on slopes, 2450 m, 27 Aug 1989, *Nesom 7192* (MEXU, TEX); ca. 5 mi S of Tanquecillos on road between San Rafael Jct & Galeana, 27 Aug 1989, *Nesom 7194* (TEX); ca. 9 km S of San Rafael along Hwy 57 toward San Rafael Jct, broad valley (Valle de Potosí), gypseous soil, area mostly cultivated, 18 Sep 1993, *Nesom 7587* (MEXU, MO, TEX); ca. 2.6 mi W of 18 de Marzo, on road to Cerro Potosí, limestone rockland with gypsum, *Pinus*, *Quercus*, *Arbutus*, 7600 ft, 25 Oct 1981, *Poole 2490* (MEXU); 20.6 mi N of San Roberto Jct on Hwy 57, 12 Oct 1984, *Sundberg 3131* (TEX, WIS). **Mpio. Iturbide**: Iturbide to Agua Blanca, edge of cultivated field, 1460 m, 21 Aug 1991, *Hinton et al. 21193* (GBH, MEXU); La Purisima to Bella Vista, oak and pine woods, 1700 m, 6 Sep 1991, *Hinton et al. 21428* (GBH).

Figure 16. *Grindelia turneri*, from isotype, *Nesom 7189* (RM).

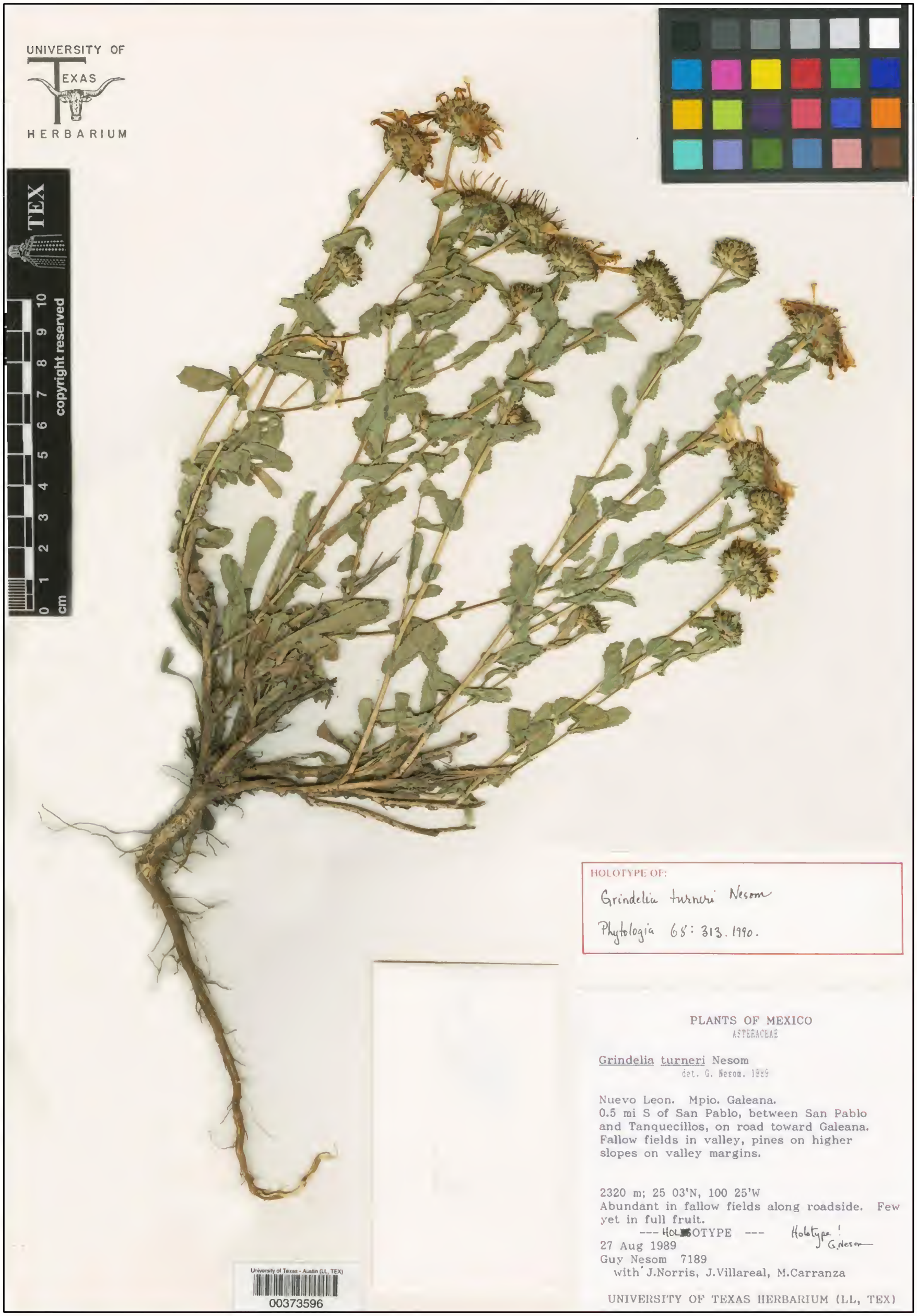

Figure 17. *Grindelia turneri*, holotype, Mpio. Galeana, *Nesom 7189* (TEX).

Figure 18. *Grindelia turneri*, Mpio. Galeana, north of San Pablo, *Hinton 27192* (GBH).

Figure 19. *Grindelia turneri*, Mpio. Galeana, north of San Pablo, *Hinton 28344* (GBH).

GRINDELIA HINTONIORUM Nesom, Phytologia 68: 328. 1990. **TYPE**: **MEXICO**. **Nuevo León**. Mpio. Galeana: 5 km E of Pablillo, oak woods, 1940 m, 15 May 1984, *Hinton et al. 18666* (holotype: TEX; isotypes: GBH, MEXU, NY, WIS).

Flowering Jul–Oct (–Nov). Llanos, meadows in pine woods areas, limestone; 2000–2500 m.

Grindelia hintoniorum is characterized by relatively short, unbranched or few-branched stems arising from a taproot, leaves with epunctate surfaces and teeth with acute, eglandular apices, and pappus awns 2–3, as long or slightly longer than the disc corollas. Stems and leaves of the type are densely stipitate-glandular but the glandularity is variable and less dense on other collections (e.g., stems and leaves are densely short-villous-pubescent and eglandular on *Pennell 17006* and *Taylor 24*; on *Pennell 17098*, stems are sparsely villous and eglandular, leaves are glabrate). Mature achenes essentially smooth-surfaced. *Grindelia hintoniorum* is similar in duration and habit to *G. turneri* and both produce elongate pappus awns. The two species apparently are allopatric/parapatric.

Most of the collections of *Grindelia hintoniorum* have been from the vicinity of Pablillo. The collection from San José de las Joyas (just north of Cerro Potosí) is separated by about 25 miles from the Pablillo system but shares the diagnostic features — George Hinton (pers. comm, Oct 28 2019) notes that the San José de las Joyas llano has now been turned completely to agriculture and that grindelias no longer exist there.

Additional collections. **MEXICO**. **Nuevo León.** Mpio. Galeana: Campos de Encinal, abundante en praderas y lomas cerca de Encinal [1 mi E of Pablillo], 1934, *Herbario Inst. de Biologia 8833* (MEXU-2 sheets); San José de Las Joyas, vast colonies in llano, 2500 m, 23 Jul 1983, *Hinton et al. 18531* (GBH); Pablillo to El Carrizo, meadow in pine woods, 2036 m, 26 Aug 2000, *Hinton et al. 27661* (GBH, MEXU); E of Pablillo, llano at edge of cultivated field, 2018 m, 30 Oct 2009, *Hinton et al. 29061* (GBH); "Encinal," Pablillo, SE of Galeana, 26-30 Jun 1934, *Pennell 17006* (PH); "Cieneguillas," Pablillo, SE of Galeana, grassy woods, 2450-2550 m, 28-30 Jun 1934, *Pennell 17098* (PH); Hacienda Pablillo, 31 Jul 1936, *Taylor 24* (MEXU, PH).

Figure 20. *Grindelia hintoniorum*. Mpio. Galeana, San José de Las Joyas, *Hinton 18531* (GBH).

Figure 21. *Grindelia hintoniorum*, Mpio. Galeana, east of Pablillo, *Hinton 29061* (GBH).

Figure 22. *Grindelia hintoniorum*, Mpio. Galeana, Pablillo to El Carrizo, *Hinton 27661* (GBH).

Figure 23. *Grindelia hintoniorum*. Mpio. Galeana, Encinal, E of Pablillo, *Herbario Inst. de Biologia 8833* (MEXU).

Figure 24. *Grindelia hintoniorum* from the Pablillo area, 27 October 2019. Photo by George Hinton.

Figure 25. *Grindelia hintoniorum* from the Pablillo area, 27 October 2019. Photo by George Hinton.

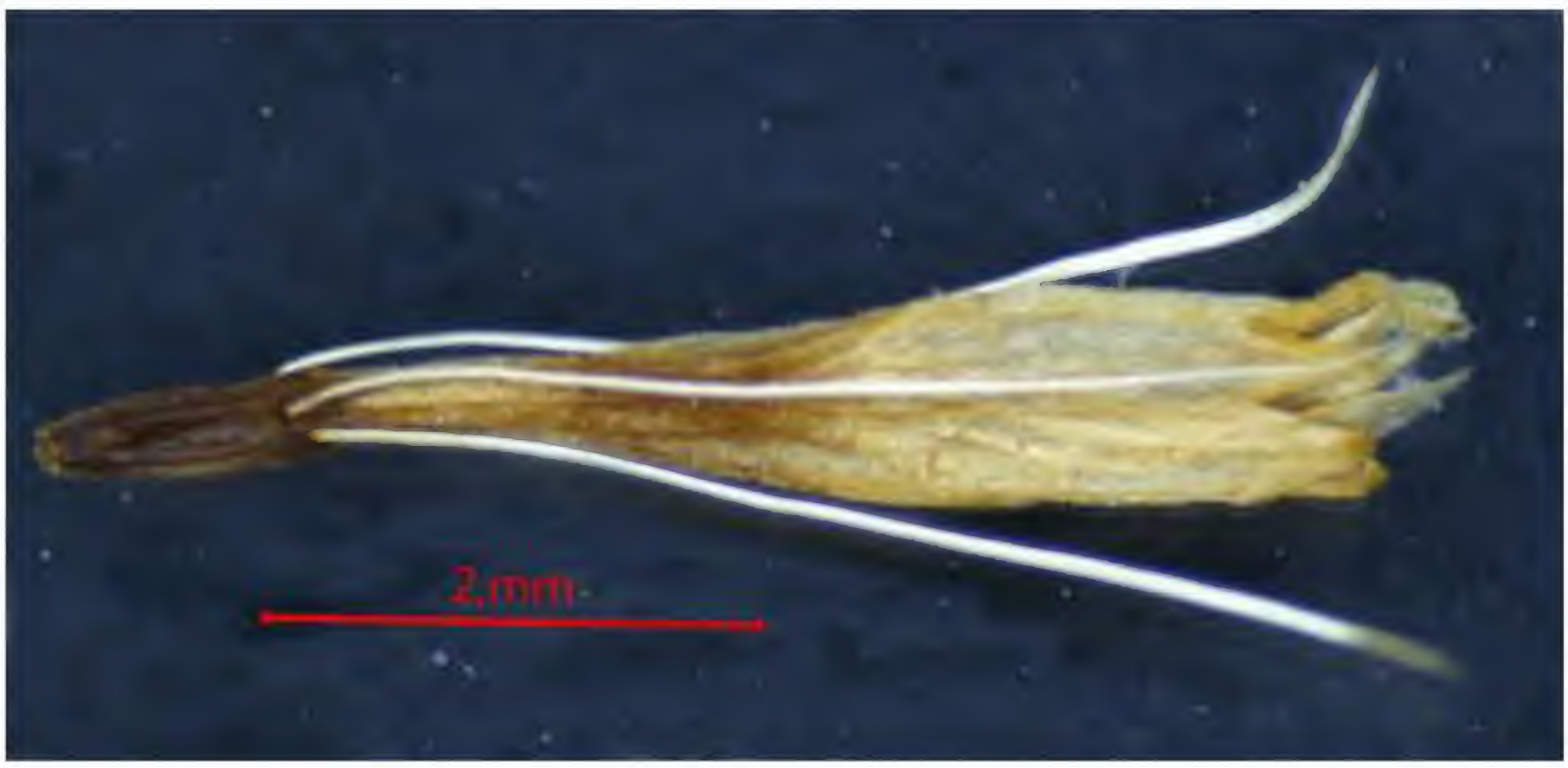

Figure 26. *Grindelia hintoniorum* from isotype: disc corolla, maturing achene, and pappus awns, *Hinton 18666* (GBH). Photo by George Hinton.

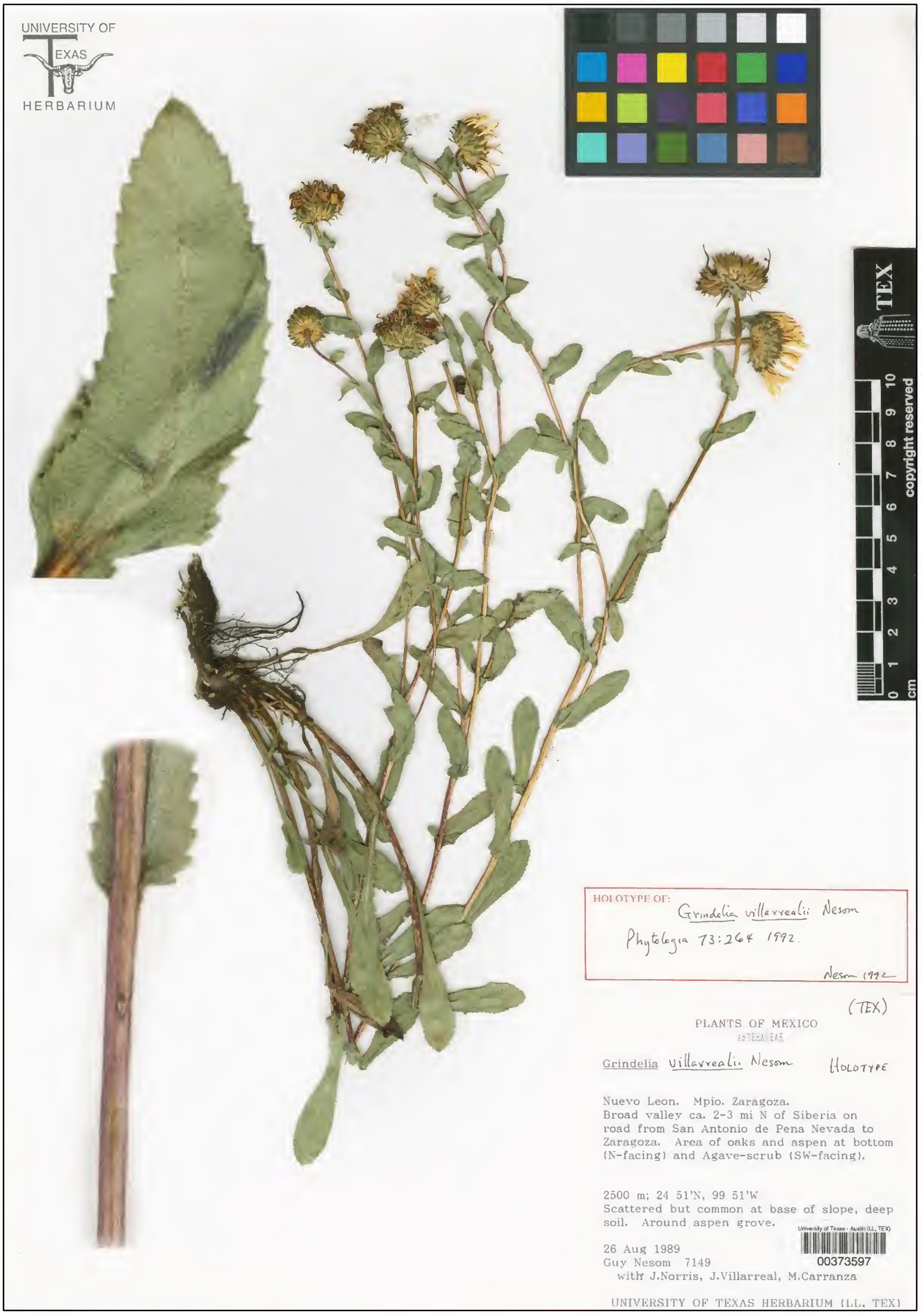

Figure 27. *Grindelia villarrealii*, holotype. Mpio. Gral. Zaragoza, Peña Nevada area. Details show acute leaf teeth and glabrous stem.

Figure 28. *Grindelia villarrealii*, Mpio. Gral. Zaragoza, Peña Nevada area. A. *Nesom 4800* (MEXU). B. *Nesom 7105* (MEXU). Collector's label observations for 7105 note that the plants were "taprooted with numerous, ascending stems from the base."

Figure 29. *Grindelia villarrealii*, from isotype (ANSM). Mpio. Gral. Zaragoza, Peña Nevada area.

Figure 30. *Grindelia villarrealii*, from isotype (ANSM). Mpio. Gral. Zaragoza, Peña Nevada area. Leaf teeth with acute, non-glandular apices.

Figure 31. *Grindelia villarrealii*, from isotype (ANSM). Taproot.

GRINDELIA VILLARREALII Nesom, Phytologia 73: 264. 1992. **TYPE**: **MEXICO**. **Nuevo León**. Mpio. Zaragoza: Ca. 2-3 mi N of Siberia on road to Zaragoza from San Antonio de Peña Nevada, broad valley, ca. 2500 m, area of oaks and aspen at the bottom (N-facing margin) and agave-scrub on the SW-facing slope, plants around the aspen grove, scattered but common at base of slope in deep soil, 26 Aug 1989, *G.L. Nesom 7149* (holotype: TEX; isotypes: ANSM, MEXU).

Flowering Jul–Sep. Margins of cultivated areas and disturbed sites, oak woods with juniper, *Nolina*, pine woods, fir woods; 2500–3050 m.

Grindelia villarrealii is characterized by perennial, taprooted, relatively tall plants (30–50 cm) with glabrous to glabrate stems. Leaves are gradually reduced distally, not forming foliaceous involucral bracts, with glabrous to minutely glandular-puberulent surfaces and acute-indurate, non-glandular teeth. Phyllary apices are triangular and loosely erect. Pappus awns are about as long as the disc corollas, with scabrous-ciliate margins.

The species is endemic to the Peña Nevada area of southeastern Nuevo Leon and immediately adjacent Tamaulipas. The only other *Grindelia* species in this area apparently is *G. obovatifolia* Blake, which is rhizomatous and with linear-filiform, recurving-recoiling phyllary apices (Figs. 12-14). *Grindelia vetimontis* occurs slightly to the north — it is rhizomatous, with villous stems and foliaceous involucral bracts.

Additional collections. **Nuevo León.** Mpio. Gral. Zaragoza: Ca. 37 km ENE of Dr. Arroyo, S-trending trail to summit of Cerro Peña Nevada beginning near road junction, zone of firs, 2700-2900 m, protected in brush, others in vicinity much smaller, 5 Aug 1983, *Nesom 4800* (MEXU, TEX); S side of Peña Nevada at "Puerto Pinos" and jct with road to Joya de San Diego, on road up from San Antonio de Peña Nevada, area of oak woods with scattered juniper, small area of cultivated fields, few plants inside fenced area, 2560 m, 23 Aug 1980, *Nesom 7105* (MEXU, TEX); 1.5 mi al NE Puerto Pinos, camino a Zaragoza, bosque esparcido de *Nolina* y plantas mésicas, cultivo de maíz, 2550 m, 24 Aug 1989, *Villarreal 4892* (MEXU). **Tamaulipas**. Mpio. Miquihuana: Along logging road E of Miquihuana on ridge SE of Cerro Peña Nevada, crest of ridge with *Pinus*, *Populus*, *Arctostaphylos*, *Quercus*, *Agave*, and *Ceanothus*, 3050 m, 1 Sep 1986, *Breedlove 63552* (MEXU, TEX); La Marcela, matorral rosetofilo, con Polyaster [*sic*], *Nolina*, *Mimosa*, 16 Jul 1990, *Mora-Olivo 02179* (MEXU).

ACKNOWLEDGEMENTS

I'm grateful to George Hinton for providing high resolution images of his full set of *Grindelia* collections and his comments on the manuscript, and to PH and BRIT for hospitality during recent study. Notes and records from earlier study at TEX were significant in preparing this manuscript.

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GEOGRAPHY OF *ERYTHRANTHE DECORA* (PHRYMACEAE)

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ABSTRACT

The occurrence of *Erythranthe decora* in Idaho and Montana is documented with collection citations and a map. These plants are disjunct nearly 200 miles eastward from the closest populations in the main part of the range in Washington and Oregon. Little or no morphological difference is apparent between the two disjunct population systems. Collections from Washington and Oregon are mapped in detail and the hypothetical distribution of evolutionary entities discovered by Coughlan et al. (2019) is shown.

The geographic range of *Eythranthe decora* (Grant) Nesom (*Mimulus guttatus* var. *decorus* A.L. Grant; *Mimulus decorus* (Grant) Suksd.) usually has been affirmed as eastern Oregon and Washington (Fig. 1). An earlier account (Nesom 2012, p. 51) noted that a UC collection from Idaho appeared to be *E. decora*, widely disjunct from the main range. Collections at PH and online images from CIC, ID, and WTU confirm the wide disjunction and show that the species in its eastern segment occurs over a relatively wide area.

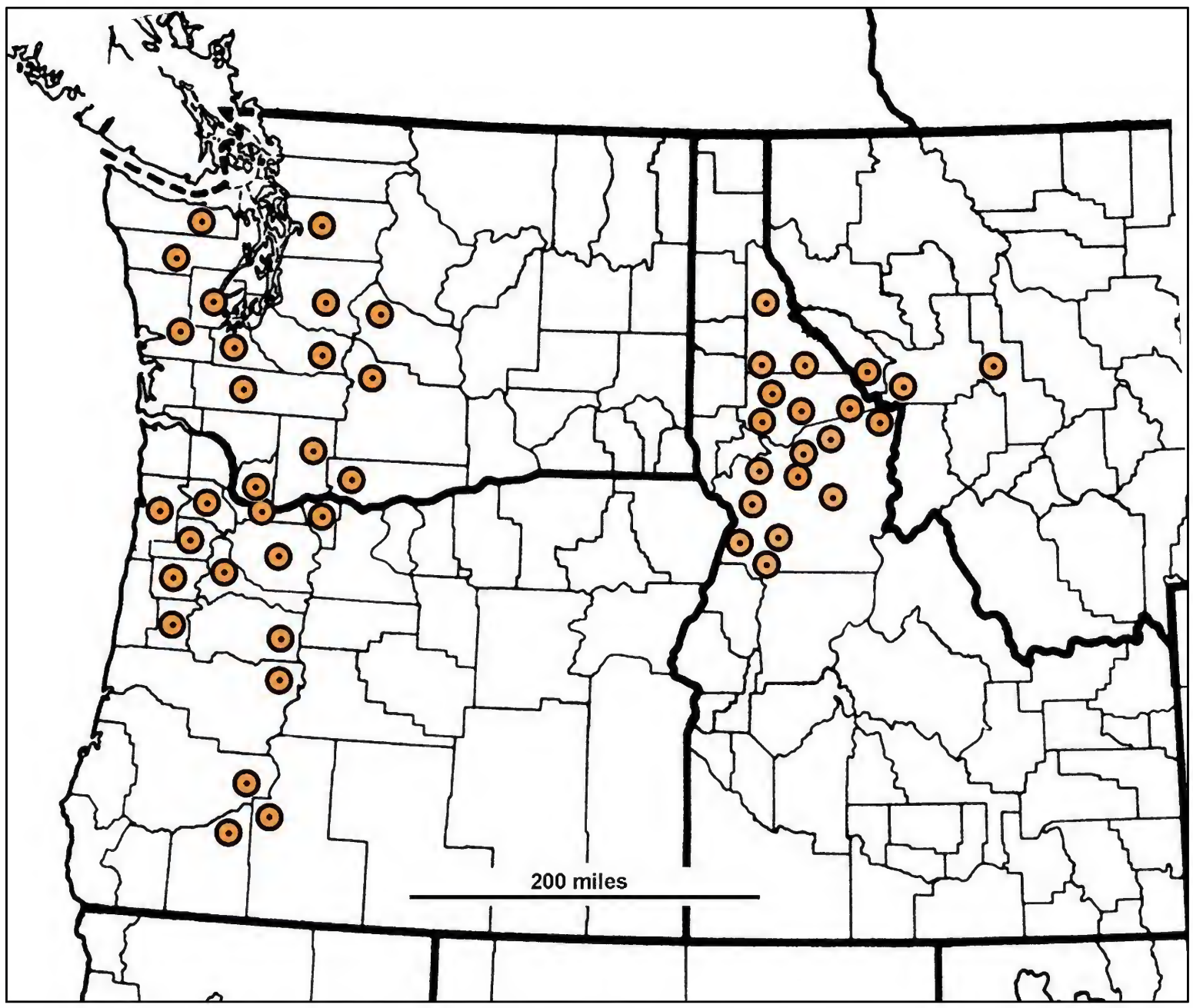

Figure 1. County-level distribution of *Erythranthe decora*. The western segment of the range is mapped with only 1 symbol per county. More localities are mapped in the eastern segment to show more detailed distribution within counties. Collections from Vancouver Island and from extreme southwestern Oregon previously identified as *E. decora* are a different species.

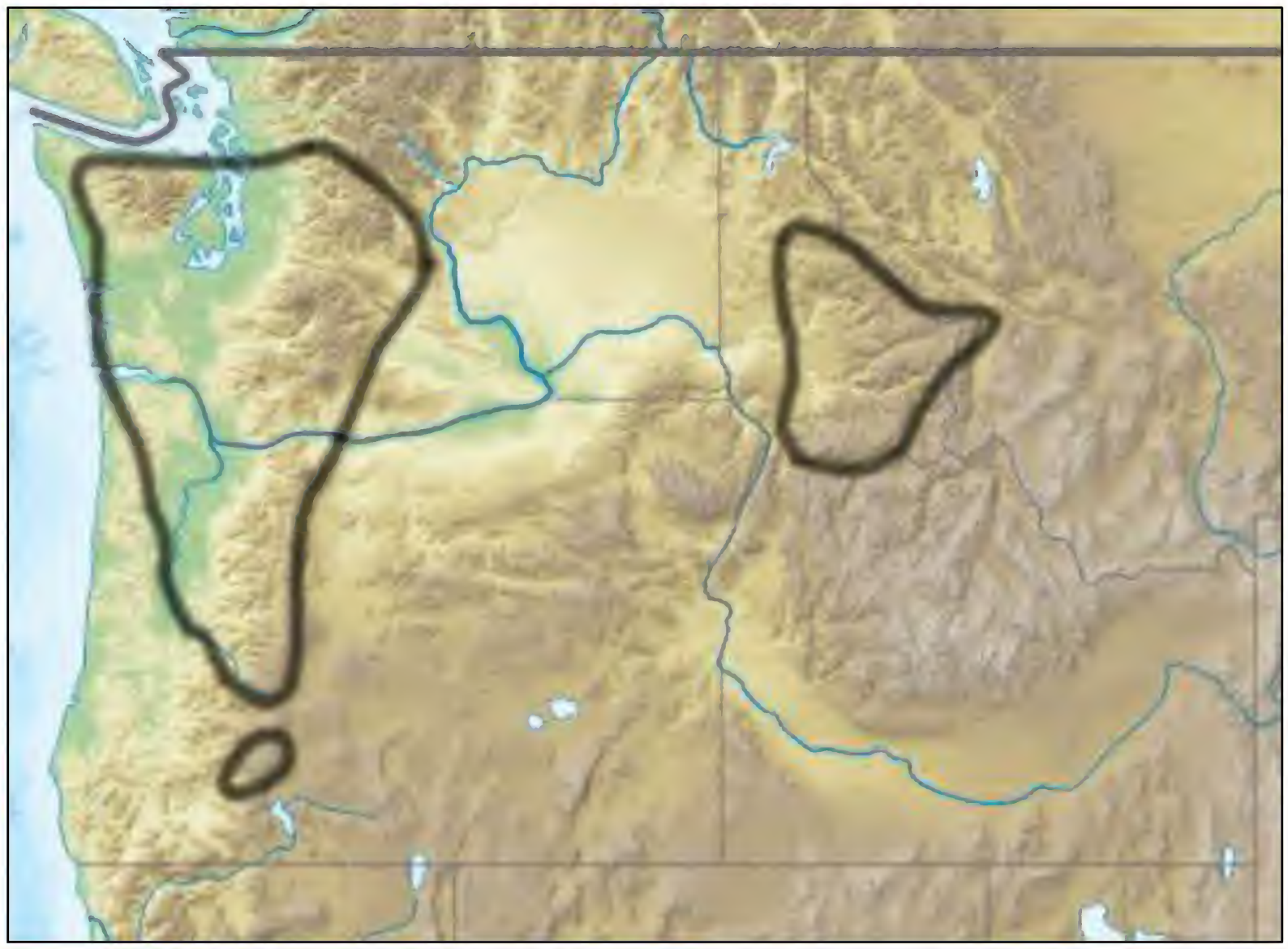

Figure 2. Distribution of *Erythranthe decora* (generalized from Figs. 1 and 5) showing the disjunction across the Columbia Plateau. The western segment of the species occurs in Coastal Ranges, the Olympic Mountains, and the Cascade Range. The eastern segment occurs in the Rocky Mountains.

Each of the PH collections cited below from Idaho and Montana was annotated in 1945 by Pennell as *Mimulus decorus*, and in a treatment of the genus for the Pacific States (Pennell 1951), he noted the distribution of the species as "coastal Washington and Oregon, east to northern Idaho." Although some floristic accounts have continued to recognize the presence of the species in Idaho (e.g., Hitchcock & Cronquist 2018; apparently following Pennell's notice in 1951; but not Davis 1952), collections of *Erythranthe decora* from there have been identified (by the author and others) as *E. guttata*, and *E. decora* has not appeared in pertinent databases.

The concept here of *Eythranthe decora* is the same as Pennell's and his annotations of PH collections initially confirmed (in the present study) the existence of the geographic disjunction. Although the characteristic stem, pedicel, and calyx vestiture (e.g., Fig. 2) is not visible in the images, collections from CIC, ID, and WTU (via the Consortium of Pacific Northwest Herbaria) are included here on the basis of the habit and perennation, characteristic leaf morphology, and large flowers, matching the features of the PH and UC specimens and standing apart from *E. guttata* in the same region (key couplet below). Figures 6-10 show representative collections of *E. decora* from Washington state; figures 11-17 show representative collections from Idaho and Montana.

1. Perennation via rhizomes; stems, pedicels, and calyces sparsely to densely, minutely and evenly hirtellous, eglandular; leaf blades ovate, bases truncate to rounded or shallowly cordate, abaxial surface (at least of distal leaves) minutely hirtellous (use lens); calyces 5.5–8 mm wide (pressed), lobes obtuse; corolla tube 15–20 mm long, 8–10 mm wide (pressed) ..... **Erythranthe decora**

1. Perennation via stolons arising from lowermost stem nodes, becoming rhizomatous; stems, pedicels, and calyces glabrous to sparsely hirtellous or hirsute-pubescent, pedicels minutely stipitate-glandular at least near the calyces; leaf blades elliptic-ovate, bases attenuate, abaxial surfaces glabrous; calyces 3.5–6 mm wide (pressed), lobes acute; corolla tubes 12–15 mm long, 4–6 mm wide (pressed) .. **Erythranthe guttata**

Morphological identity between plants in the western and eastern segments of the range suggests that they can be considered a single species. A possible difference is in corolla markings — corolla throats of the Idaho-Montana plants sometimes dry with a distinctive blue-green color (e.g., see Figs. 13, 14, 16), suggesting a strongly differentiated bulls-eye UV nectar guide (Peterson et al. 2015). This coloration has not been observed in collections of western *E. decora*. The two geographic systems appear to be similar in ecology, although the eastern plants do not range as low in elevation — the eastern plants occur at 2450–5500(–6400) feet and are usually in wet meadows and seeps, along wet stream banks, or on wet rock faces and cliffs. In any case, the wide disjunction between two large population systems suggests that genetic differentiation probably has occurred, even if it does not influence apparent morphology or habitat.

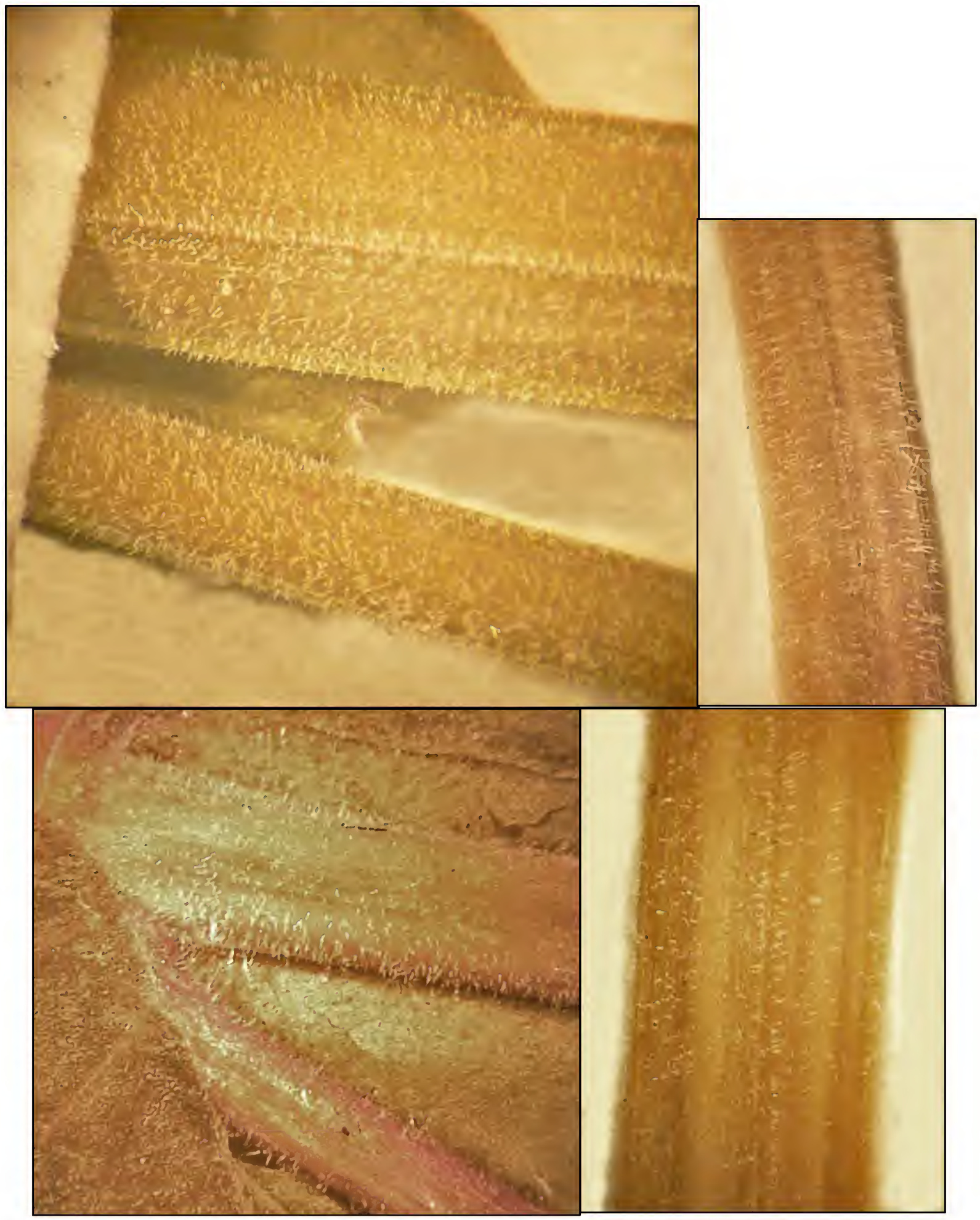

Figure 3. *Erythranthe decora*, representative stem and pedicel vestiture.

Erythranthe decora in Idaho and Montana.

Idaho. Clearwater Co.: Near Jaype, 3 Jul 1946, *Joslyn 342* (ID); near Hollywood, between Jaype and Pierce, meadow, 3 Jul 1946, *Joslyn 343-346* (WTU); wooded tributary of Clearwater River, along FS Road 1705, ca. 2-3 mi E of Granddad Bridge, *Alnus*, *Thuja*, *Acer*, *Tsuga*, *Pseudotsuga*, 2296 ft, 17 Jun 2003, *Parks 377* (ID); Morris Creek drainage, near headwaters of Morris Creek and Old Growth Cedar Grove, along FRd 1969d, 0.5 mi from jct of FRd 1969, ca. 1.3 air mi N of Shattuck Butte, 12.2 mi NNE of Elk River by road, riparian area along Morris Creek dominated by *Carex* sp., *Phalaris arundinacea*, and *Alnus* sp., 4300 ft, plants occasional along wet stream banks, 21 Jul 1996, *Richardson 478* (ID, UC); Pierce, 4 Jul 1939, *Stillinger 556* (ID). Idaho Co.: Lolo Pass, North Meadow, 30 Jun 1941, *Davis 3697* (IDS, PH); California Creek, cold springs, wet seep, 5000 ft, 25 Jun 1930, *Gray 67344* (CIC); Nez Perce Natl Forest, 1.3 mi W on Swiftwater Road from jct with Selway River Road, W side of road, streamside mossy wet banks, 2500 ft, 25 Jun 1995, *Crockett 90* (ID); Red River Hot Springs, creek bottom at headwaters of Red River, 11 Aug 1954, *Baker 12407* (ID, WTU); Grave Creek Canyon, 6 mi N of the Salmon River, wet rocky cliffs, 7 Jun 1960, *Baker 15841* (ID); along the McClinery Ridge Road 517 at its jct with the S Fork of Papoose Creek (at the upper or 4th crossing), 6400 ft, rocky creek bottom along roadside, 17 Aug 1982, *Bingham & Miller 570* (ID); Clearwater Natl Forest, Lochsa River Drainage, Canyon Creek Trail 107 of Hwy 12along trail in very moist creek bottom, locally common on moist rock faces, 2475 ft, 2 Jun 2009, *Brunsfeld 6301* (ID); Snake River Canyon, Sheep Creek 1/2 mi above its mouth, springy places on rocky N slope, 13 May 1937, *Constance et al. 1826* (WTU); Frenchman Butte, seepage in spruce-fir zone, dense *Alnus* scrub, 13 Jun 1945, *Daubenmire 4583* (WTU); Nez Perce Natl Forest, between Orogrande and Dixie, common along Moose Meadow Creek just upstream from jct with Big Creek, ca. 2 mi SSE of Badger Summit, 19 Aug 1976, *Henderson et al. 3526A* (ID); N of Elk City, head of West Fork of American River, cold brook sides, 4800-4900 ft, 2 Jul 1937, *Pennell 20865* (PH); N of Elk City, head of West Fork of American River, cold brook sides, 5300-5400 ft, 2 Jul 1937, *Pennell 20867* (PH); Hwy 95, Whitebird grade, 1/5 mi N of mile marker 228, base of Columbia River, basalt face, occasional in rocks, ca. 4630 ft, 22 May 2008, *Poor 16* (ID); Clearwater, Powell Ranger Station, 1932, *Rust 1985* (ID); Hazard Lakes, near summit of Bruin Mtn, 13 Aug 1934, *Tucker 141* (CIC, ID); along East Fork of Papoose Creek, very moist borrow pit off road, Thupli/Pacmyr H.T., 3600 ft, 30 Jun 1974, *Wellner 197* (ID). Shoshone Co.: 5 mi E of Clarkia on Gold Center Creek road, grazed meadow near St. Maries River, 23 Jun 1968, *Bobisud 885* (ID); Bitterroot Range, Clearwater Natl Forest, N side of Chamberlain Meadows, ca. 2.5 air mi ESE from Five Lakes Butte along Vanderbilt Trail, rare in wet depressions near main stream channel, 5450 ft, 6 Aug 1987, *Henderson 7382* (ID); near Clarkia, near Grandfather Creek, Potlatch ownership, wet meadow, 3158 ft, 17 Jun 2009, *Longworth 29* (ID).

Montana. Mineral Co.: Lolo Natl Forest, between Irish and Cache Creek, edge of stream, small pocket near summit of Continental Divide, 13 Aug 1933, *Hitchcock 2118* (PH); subalpine area on Hoodoo Creek near pass, glacial cirque area, large wet meadows along creek, 28 Jul 1971, *Mooar 13,757* (MONTU); Great Burn Proposed Wilderness Area, near a seep on the SE end of Pearl Lake, in a 75+ year-old subalpine forest burn still in the shrub-herb stage, 40+ individuals restricted to the vicinity of the seep, 6320 ft, 25 Aug 1985, *Mooers 1051* (MONTU). Missoula Co.: Stream banks of East Fork of Lolo Creek, marshy and mossy areas, 19 Jul 1970, *Mooar 12,757* (MONTU). Powell Co.: Clearwater Forest, Chamberlain meadows, 5300 ft, 5 Jul 1916, *Devan 83* (PH).

Coughlan et al. (2019 – their data mapped here in Figure 3) found that diploids and tetraploids occur within *Erythranthe decora* (the western segment of the range) and that two geographic clades (evidence from crossing data) exist among the diploids. Strong post-zygotic reproductive barriers (hybrid seed inviability) exist between the northern and southern diploids and between each of these and the tetraploids. The three races appear to be indistinguishable in morphology (personal observation).

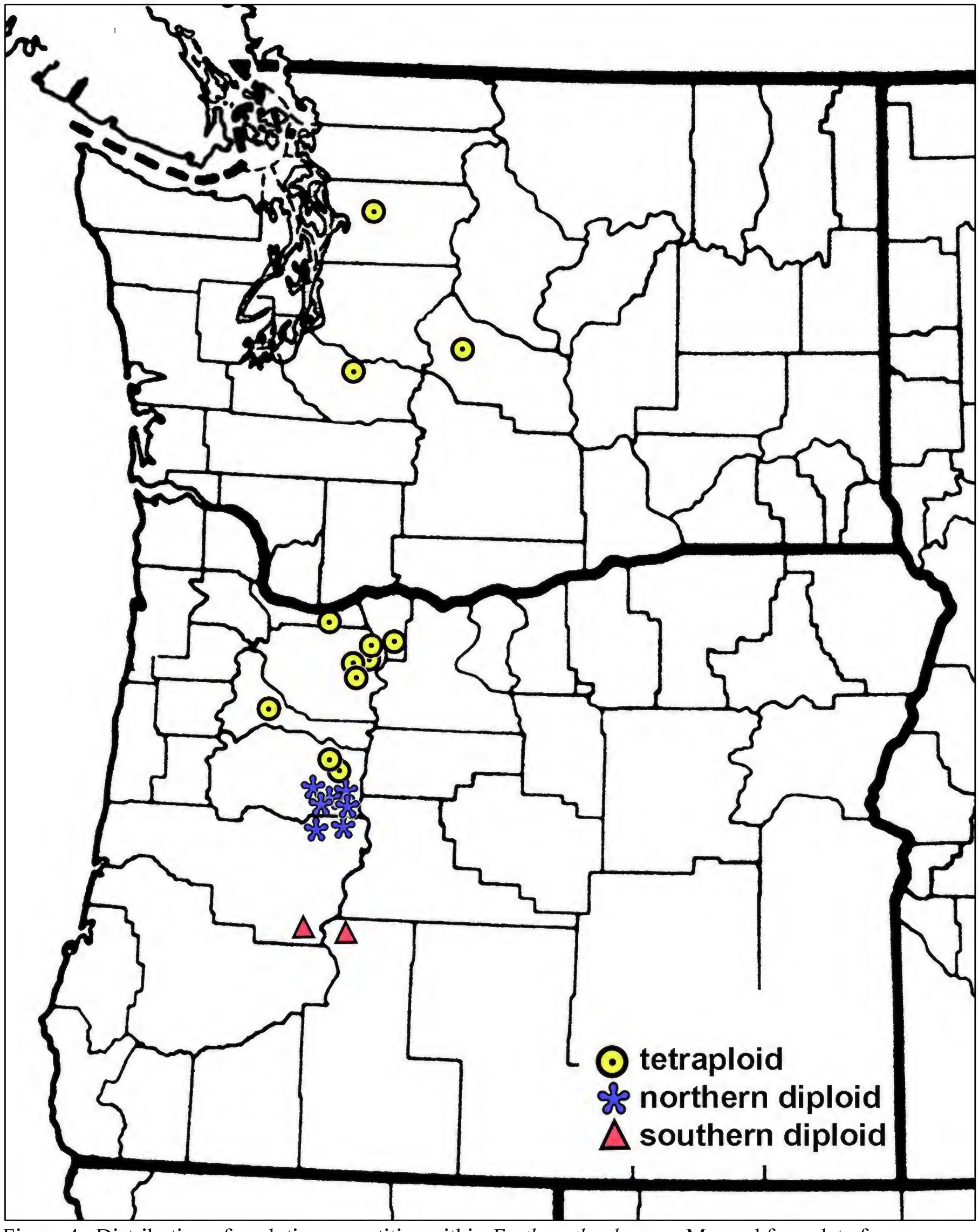

Figure 4. Distribution of evolutionary entities within *Erythranthe decora*. Mapped from data from Coughlan et al. (2019, Supplemental Table 2), reporting chromosome counts from 21 populations. Localities were precisely given as geographic coordinates, but no vouchers were cited.

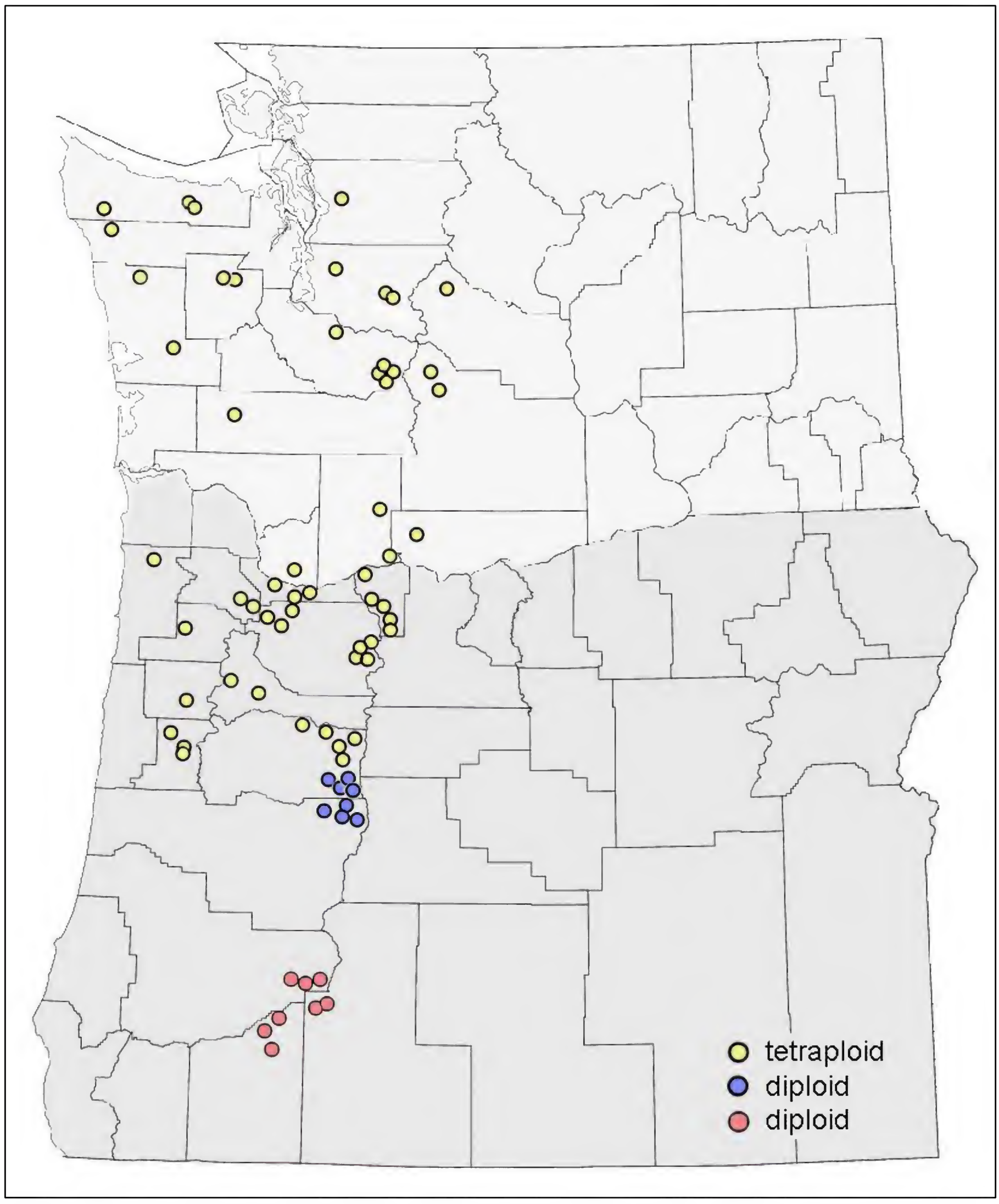

Figure 5. Distribution of *Erythranthe decora* in Washington and Oregon, mostly from records in WTU, OSC, and PH. Colors show hypothetical distribution of entities discovered by Coughlan et al. (2019; compare with Figure 3).

Figure 6. *Erythranthe decora*, representative collection. **Washington**. Clallam Co.: *Meyer 1017* (WTU).

Figure 7. *Erythranthe decora*, representative collection. **Washington**. Jefferson Co.: *Otis 1310* (WTU). Exceptionally large leaves.

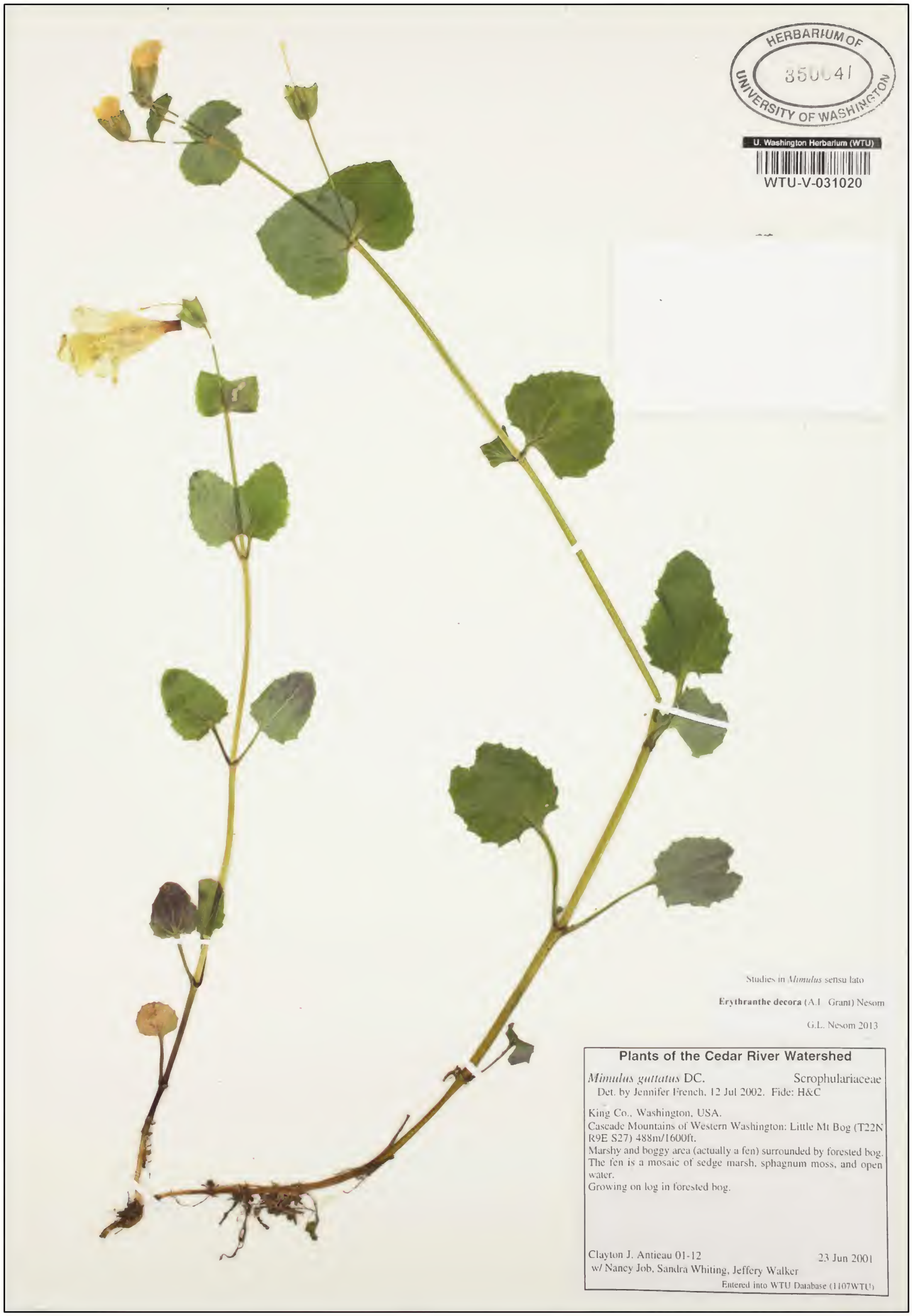

Figure 8. *Erythranthe decora*, representative collection. **Washington**. King Co.: *Antieau 01-12* (WTU).

Figure 9. *Erythranthe decora*, representative collection. **Washington**. Pierce Co.: *McCalla 5155* (UBC).

Figure 10. *Erythranthe decora*, representative collection. **Washington**. Skamania Co.: *Suksdorf 2774* (WTU).

Figure 11. *Erythranthe decora*, representative collection. **Idaho**. Clearwater Co.: *Joslyn 342* (ID).

Figure 12. *Erythranthe decora*, representative collection. **Idaho**. Clearwater Co.: *Joslyn 343-346* (WTU).

Figure 13. *Erythranthe decora*, representative collection. **Idaho**. Clearwater Co.: *Parks 377* (ID).

Figure 14. *Erythranthe decora*, representative collection. **Idaho**. Idaho Co.: *Crocket 90* (ID).

Figure 15. *Erythranthe decora*, representative collection. **Idaho**. Shoshone Co.: *Longworth 0029* (ID).

Figure 16. *Erythranthe decora*, representative collection. **Montana**. Missoula Co.: *Mooar 12,757* (MONTU).

Figure 17. *Erythranthe decora*, representative collection. **Montana**. Mineral Co.: *Mooers 1051* (MONTU).

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RECOGNITION OF *ERYTHRANTHE VERONICIFOLIA* (SECT. *SIMIOLUS*; PHRYMACEAE)

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ABSTRACT

Plants described by Greene in 1909 and treated by Pennell in 1951 as *Mimulus veronicifolius* are belatedly recognized here as distinct, as **Erythranthe veronicifolia** (Greene) Nesom, **comb. nov.** The species is endemic to high elevations in the Olympic Mountains of northwestern Washington and Vancouver Island. It similar to and probably most closely related to *Erythranthe decora* of sect. *Simiolus*.

Study of *Erythranthe decora* (Nesom 2019) has led to the recognition of a distinct, more narrowly distributed species probably closely related to it. These plants were described by Greene in 1909 and treated by Pennell in 1951 as *Mimulus veronicifolius* — the species is here brought into *Erythranthe* (sect. *Simiolus*).

Erythranthe veronicifolia (Greene) Nesom, **comb. nov.** *Mimulus veronicifolius* Greene, Leafl. Bot. Observ. Crit. 2: 7. 1909. **TYPE**: **USA**. **Washington**. [Clallam Co.:] Olympic Mountains, along rivulets, 5000 ft, Aug 1895, *C.V. Piper 2177* (holotype: ND-Greene!). Figure 3.

Plants perennial from slender rhizomes. **Stems** erect, 10–30 cm tall, glabrous proximally, becoming sparsely minutely hirtellous distally. **Leaves**: basal very small, largest at midstem, blades elliptic-ovate, 10–30(–45) mm long, base attenuate to a petiole or petiolar region 5–15 mm (proximal leaves) to 0–3(–5) mm (mid and distal leaves) long, margins shallowly serrate to crenate with 5–8 teeth per side, both surfaces glabrous. **Flowers** 1–3(–7) from distal nodes. **Fruiting pedicels** 20–40 mm. **Calyces** 10–15 mm long, densely minutely hirtellous, rarely purple-spotted (variable within populations), lobes obtuse. **Corollas** yellow to chrome yellow, without red spots, tube-throat 15–25 mm long, 8–12 mm wide (pressed), exserted 15–25 mm beyond the calyx margin, limb expanded 18-25 mm (pressed).

Flowering (Jun–) Jul–early Sep. Boggy alpine meadows, around springs and rivulets, lake sides and along rocky streams; 3000–5700 feet. Figure 10 shows an Olympic Mountains colony in situ.

Additional collections. **CANADA**. **British Columbia**. Vancouver Island: Port Alberni, Limestone Mtn., end of logging road M2A, between Limestone Mtn. and Mt. McQuillam, 900 m, 8 Jul 1983, *Ceska et al. 15208* (UBC); Forbidden Plateau, 1936, *Fowle s.n.* (UBC); Strathcona Park, Burman Lake, [ca. 4900 ft], 10 Aug 1958, *Krajina et al. 68081017* (UBC); Sproat Lake, alpine meadow, 3300 ft, 10 Aug 1941, *Taylor 1267* (UBC); Moat Lake, 4000 ft, 26 Jul 1957, *Underhill 338* (UBC). **USA**. **Oregon**. Clallam Co. [Olympic Mts., Olympic Natl Park]: Hurricane Hill, in cañon near top of ridge about spring, 5000 ft, 16 Aug 1941, *Foster 1904* (PSU); Boulder Creek, 6 Sep 1935, *Jones 8487* (WTU); E side of Obstruction Point, along very moist rivulets, 5700 ft, arctic-alpine zone, 4 Sep 1937, *Meyer 1247* (WTU); Mt. Angeles, rocky stream, 4800-5200 ft, 9 Aug 1931, *Pennell 15821* (PH); Deer Lake, above Duc Hot Springs, boggy meadow, 3600-3700 ft, 9 Aug 1937, *Pennell & Meyer 21214* (PH); Hurricane Ridge, E of Elwha River, cold, shaded swamp, 3400-3500 ft, 11 Aug 1937, *Pennell & Meyer 21267* (PH); Mt. Angeles, wet stream banks, 5100 ft, 2 Aug 1930, *Thompson 5531* (PH); near summit of Mt. Angeles, wet bank of alpine stream, 5100 ft, 2 Aug 1930, *Thompson 5541* (WTU); Mt. Angeles, swampy alpine meadow, 5000 ft, 19 Jun 1931, *Thompson 7555* (PH, WTU); Mt. Angeles, moist stream banks, 5500 ft, 10 Aug 1931, *Thompson 7849* (PH, WTU); Mt. Angeles, 14 Aug 1911, *Webster 1945* (WTU).

Erythranthe veronicifolia is recognized by its rhizomatous habit, erect, mostly unbranched stems minutely hirtellous distally, glabrous proximally, relatively long internodes, ovate-lanceolate

leaves with shallowly serrate-crenate margins and attenuate base, and few flowers with large corollas. Greene (1909) noted that the corollas were "perhaps the largest in the genus." Plants of the species are remarkably constant in morphology (Figures 3-9).

Grant (1924) placed *Mimulus veronicifolius* as a synonym of *Mimulus tilingii* var. *corallinus*. Pennell (1951) recognized *M. veronicifolius* as a distinct species endemic to the Olympic Mountains, comparing it in his key to *M. decorus*. I placed *M. veronicifolius* in 2012 as a synonym of *Erythranthe caespitosa* and, reflecting my confusion about its identity, have annotated collections of it as *Erythranthe tilingii* (emphasizing the rhizomatous habit and leaf shape), more recently as *Erythranthe decora* (emphasizing vestiture). Other floristic accounts either have not included *E. veronicifolia* (e.g., Hitchcock & Cronquist 1973, 2018) or have treated it as a synonym of *E. tilingii* (e.g., Campbell 1950; Klinka & Qian 2002). On review of morphological and geographic variation in *E. decora* (Nesom 2019), the distinction of *E. veronicifolia* has become apparent. The two are contrasted here.

a. Stems 30–100 cm tall; leaf blades broadly ovate-triangular to ovate-lanceolate with truncate to rounded or shallowly cordate base, mostly 3–5(–6) cm long, with 9–15 teeth per side, smaller teeth often between larger; midstem petioles 3–5 mm long ..... **Erythranthe decora**

a. Stems 10–30 cm tall; leaf blades elliptic-ovate with attenuate base, 1–4.5 cm long, with 5–8 even-sized teeth per side; midstem petioles 0–3(–)5 mm long ..... **Erythranthe veronicifolia**

In both species, pedicels and calyces characteristically are minutely hirtellous. Stems of *Erythranthe decora* also are hirtellous, at least distally; distal stems of *E. veronicifolia* are hirtellous but sometimes glabrate with only a few scattered hairs. The abaxial leaf surface (less commonly both surfaces) of distal leaves of *E. decora* is minutely hirtellous (often seen only with a lens), while both surfaces of *E. veronicifolia* consistently are glabrous.

Erythranthe veronicifolia has been commonly collected in the Mt. Angeles area of the Olympic Mountains — typical *E. decora* occurs there sympatrically (e.g., Mink Lake above Sol Duc Hot Springs, *Pennell & Meyer 21228*, PH). Typical *E. caespitosa* also occurs on Mt. Angeles (e.g., *Thompson 5540*, PH) — some plants may resemble small individuals of *E. veronicifolia* (with short stems, small leaves), but *E. caespitosa* has mostly procumbent stems, smaller leaves with fewer teeth, glabrous calyces, and smaller corollas.

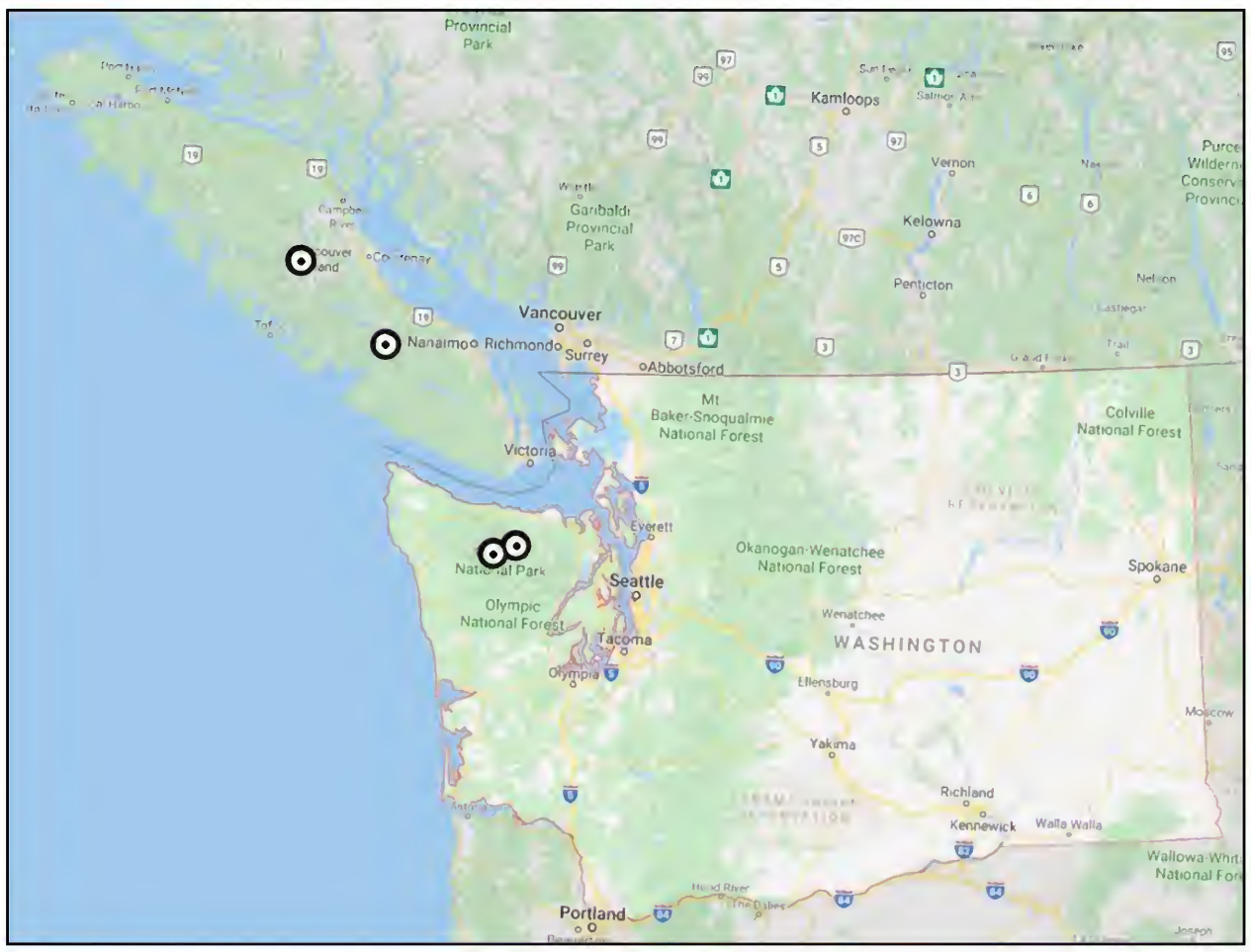

Figure 1. Distribution of *Erythranthe veronicifolia*. Detailed localities are shown in Fig. 2.

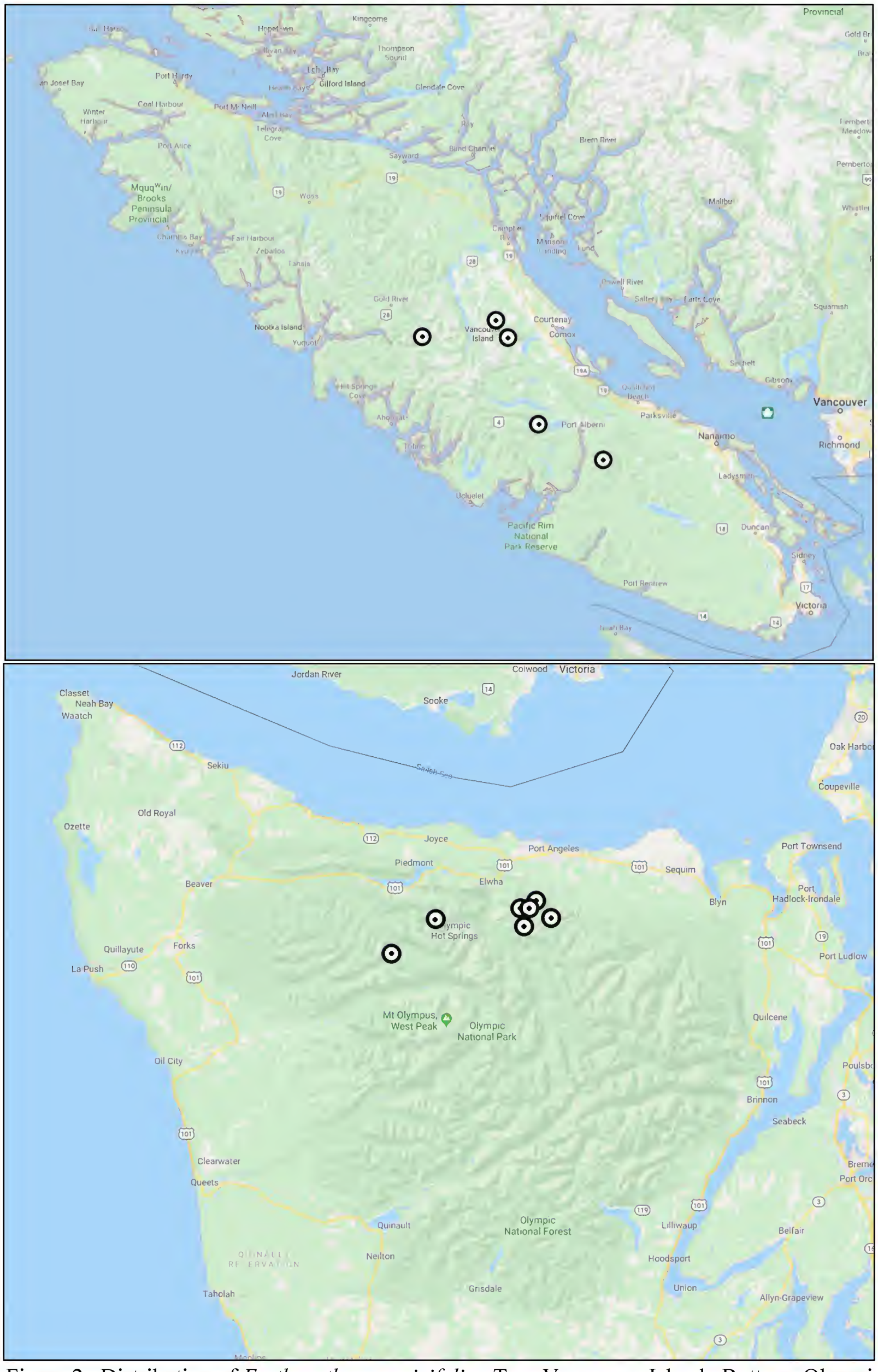

Figure 2. Distribution of *Erythranthe veronicifolia*. Top: Vancouver Island. Bottom: Olympic Mountains.

Figure 3. *Erythranthe veronicifolia*. Olympic Mountains, holotype, NDG.

Figure 4. *Erythranthe veronicifolia*. Olympic Mountains, *Thompson 7849*, WTU.

Figure 5. *Erythranthe veronicifolia*. Olympic Mountains, *Thompson 7555*, WTU.

Figure 6. *Erythranthe veronicifolia*. Olympic Mountains, *Jones 8487*, WTU.

Figure 7. *Erythranthe veronicifolia*. Vancouver Island, *Ceska et al. 15208* (UBC).

Figure 8. *Erythranthe veronicifolia*. Vancouver Island, *Taylor 1267* (UBC).

Figure 9. *Erythranthe veronicifolia*. Vancouver Island, *Underhill 338* (UBC).

Figure 10. *Erythranthe veronicifolia* in Olympic National Park. "Moist area near the trailhead for the switchback trail up the south side of Klahhane Ridge" (Slichter 2016). Photo by Paul Slichter, 26 July 2014, used by permission. Klahhane Ridge is between Mt. Angeles and Rocky Peak, about 1 mile west of Mt. Angeles.

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UNA NUEVA ESPECIE DE *PINGUICULA* (LENTIBULARIACEAE) DE HONDURAS

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RESUMEN

Se describe e ilustra ***Pinguicula hondurensis*** Zamudio & H. Vega, **sp. nov.**, a partir de ejemplares provenientes del Parque Nacional Pico Bonito, en el Departamento de Atlántida y del Cerro del Diablo, Departamento de Olancho, Honduras. La especie nueva se ubica en el subgénero *Pinguicula*, sección *Longitubus*, por la corola bilabiada, con el tubo largamente infundibuliforme, más largo que los lóbulos de la corola; sin embargo, se diferencia de las especies ya conocidas de este grupo por la condición homófila (presenta un solo tipo de hojas) y la corola morada, lo que representa dos novedades en la sección; en consecuencia, se hace la enmienda de la diagnosis de la sección para dar cabida al nevo taxón. La presencia de esta especie en Honduras marca el límite sur de distribución de la sección. Adicionalmente se proporciona una clave dicotómica para la identificación de sus especies.

ABSTRACT

Pinguicula hondurensis Zamudio & Hermes Vega, **sp. nov.**, is described and illustrated from material from Pico Bonito National Park, Depto. Atlantida, and Cerro del Diablo, Depto. Olancho, Honduras. The new species belongs to subg. *Pinguicula* sect. *Longitubus*, in view of the bilabiate corolla with a long-infundibuliform tube longer than the corolla lobes. It is differentiated of all the members of the section by the homophyllous condition (with only one type of leaves) and by the purple corolla, which represent two novelties in the section; consequently an amendment of the section diagnosis is made. The presence of this species in Honduras marks the southern limit of the section. A dichotomous key is provided to the species of sect. *Longitubus*

Durante una visita al herbario del Jardín Botánico de Missouri (Missouri Botanical Garden), en octubre del año 2009, al revisar las colecciones de la familia Lentibulariaceae, con miras a la preparación de la revisión de la familia para la Flora Mesoamericana, se encontraron dos ejemplares de una colecta procedente de Honduras, correspondiente a una especie no descrita de *Pinguicula*. Aunque los especímenes representaban claramente una especie nueva, no contenían todas las estructuras necesarias para hacer una descripción completa (ej. hojas o rosetas de invierno, frutos maduros y semillas), por lo que en mayo del 2014 se realizó una expedición a Honduras con la intención de recolectar material adicional que permitiera su descripción completa. A pesar de que durante este viaje se visitaron varias localidades en busca de alguna población de las plantas, desafortunadamente éstas no se localizaron.

Al revisar el herbario Paul C. Standley, de la Escuela Agrícola Panamericana en Tegucigalpa, Honduras (EAP), se encontró una colecta adicional de la planta en flor con un solo individuo. En vista de las dificultades para recolectar el material de la especie se decidió realizar la descripción con el material disponible, la que se presenta a continuación:

PINGUICULA HONDURENSIS Zamudio & H. Vega, **sp. nov.** Figs. 1 y 2. **TIPO: HONDURAS**. **Departamento de Atlántida**. Pico Bonito National Park, "Ridge Campsite," trail leading from "Ridge Campsite" of climb to Pico Bonito, 15°38'15" N, 86°51'40" W, 2100 m. 23 Apr 1996, *T. Hawkins 906* (holotipo MO; isotipo MO).

Herba perennis; folia radicalia isomorpha, (4)6–8, subpetiolata, laminae obovatae vel ample obovatae, margine leviter involutae, 30–60 mm longae, 15–35 mm latae, petioli 3–10 mm longi; pedunculi 1–3 erecti, dense villosi prope apicis basin versus glabrescens, 120–160 mm longi; flores 30–45 mm longi (calcare incluso); calyx bilabiatus, lobis oblongo-lanceolatis vel lanceolatis, 3–4.5 mm longis, 1.2–2 mm latis; corolla bilabiata, violacea, cum lineis albis prope lobum basim, fauce alba, labium superum bilobatum, lobis obovatis, rotundatis vel leviter emarginatis, 6–12 mm longis, 8–12 mm latis, labium inferum trilobatum, lobis obovatis vel ample-obovatis, 9–17 mm longis, 5–12 mm latis, rotundatis, lobus medius lateralibus major, apice rotundatus vel emarginatus; tubus longe-infundibuliformis, 12–19 mm longus, 4–6 mm latus, intus dense pubescens, pilis cylindrico-subulatis, multicellularibus, retrorsis, palatum nullum, calcar cylindrico-subulatum, rectum, 4–6(8) mm longum; capsula ignota; semina ignota.

Planta herbácea perenne; **tallo** compacto, **rizoma** simple corto, con numerosas raíces adventicias filiformes; **hojas** agrupadas en una roseta basal laxa, de (45)50–80(100) mm de diámetro, formada por (4)6–8 hojas membranáceas adpresas al suelo, subpecioladas, peciolo menor de 1 cm, lámina obovada a ampliamente obovada, de 30–60 mm de largo, por 15–35 mm de ancho, ápice redondeado, base atenuada, margen ligeramente involuto, densamente glandular-pubescente en el haz, con glándulas estipitadas y glándulas sésiles; **pedúnculos** 1–3 por planta, erectos, rollizos, verdes o teñidos de púrpura, de 120–160 mm de largo, densamente glandular pubescentes cerca del ápice, glabrescentes hacia la base, con pelos glandulares estipitados menores de 1 mm; **flores** de 30–45 mm de largo (incluyendo el espolón); **cáliz** bilabiado, glandular pubescente en la cara externa y esparcidamente glandular en la cara interna, con pelos glandulares cortos, labio superior dividido casi hasta la base en 3 lóbulos lanceolados u oblongo-lanceolados, de 3–4.5 mm de largo, por 1.2–2 mm de ancho, ápice agudo u obtuso, labio inferior dividido casi hasta la base en dos lóbulos lanceolados, de 3–4 mm de largo, por 1–1.5 mm de ancho; **corola** bilabiada, morada, con líneas blancas en la base de los lóbulos, que se extienden hasta la garganta, garganta blanca, esparcidamente pubescente por fuera, con pelos glandulares cortos menores de 0.5 mm, labio superior 2-lobado, lóbulos obovados a suborbiculares u oblatos, de 6–12 mm largo, por 8–12 mm ancho, ápice redondeado o ligeramente emarginado, labio inferior 3-lobado, lóbulos obovados a ampliamente obovados, de 9–17 mm de largo, por 5–12 mm de ancho, ápice redondeado, el lóbulo medio notoriamente más grande que los laterales, a veces ligeramente emarginado; **tubo** largamente infundibuliforme, de 12–19 mm de largo, por 4–6 mm de ancho, sin paladar, pubescente en el interior, con un mechón denso de pelos simples multicelulares subulados, retrorsos, concentrados en la parte ventral, que disminuyen de tamaño hacia la base; **espolón** cilíndrico-subulado, recto, de 4–6(8) mm de largo, ápice agudo, glandular pubescente por fuera, con tricomas simples dispersos, glandular pubescente por dentro con pelos subulados retrorsos cortos; **ovario** subgloboso, glandular-pubescente, de 2–3 mm de diámetro, estilo subsésil, estigma bilabiado, el lóbulo superior reducido, el lóbulo inferior flabelado, de ±2 mm de largo, por ±2.5 mm de ancho, borde fimbriado; **estambres** dos, curvos, de 3 mm de largo, los filamentos arqueados de 2 mm de largo, con glándulas estipitadas cortas, anteras reniformes, de ±1 mm de largo; **cápsula** desconocida; **semillas** desconocidas.

Material adicional revisado. **HONDURAS**. **Departamento de Olancho**. Cerro del Diablo, El Carbón, alt. 1546-1897 m, 29 May 2013, *Romero 383* (EAP).

Ecología. Crece en taludes y paredes de rocas expuestas a la acción de los vientos húmedos del NE, entre el bosque mesófilo de montaña o bosque de niebla, con *Clusia*, *Cupressus, Liquidambar* y *Pinus*. Alt. 1546-2100 m.

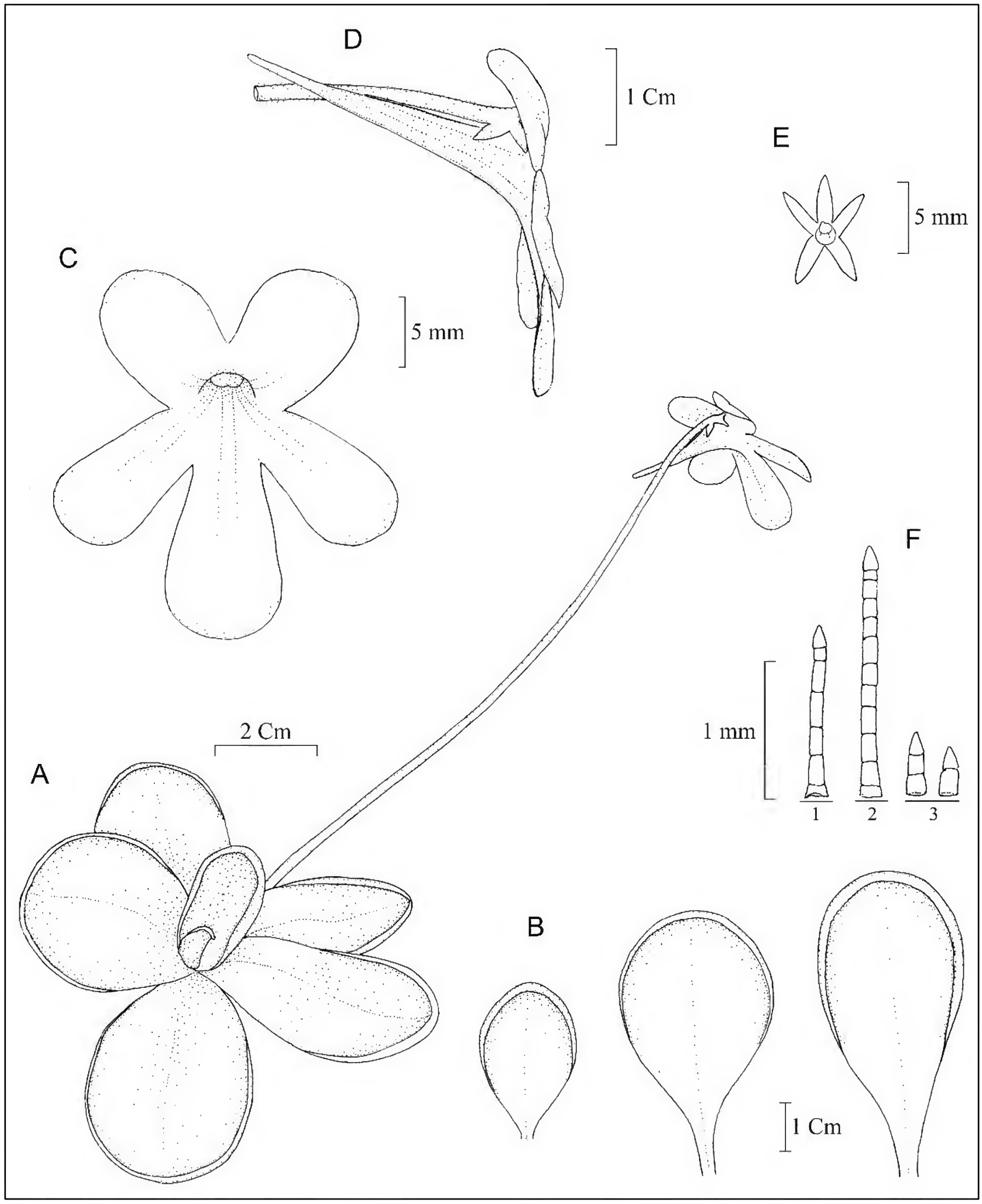

Figura 1. *Pinguicula hondurensis*. A. Hábito, roseta de hojas con flor. B. Serie de hojas. C. Flor vista de frente. D. Flor vista de lado. E. Cáliz. F. Pelos del interior de la corola; 1. De la garganta, 2. Del tubo, 3. Del espolón. Ilustrado por Manuel Ramírez Amezcua, a partir del espécimen de *T. Hawkins 906* (MO).

Figura 2. *Pinguicula hondurensis*. A. Hábito de la planta. B. Flor vista de lado, destaca el tubo de la corola largamente infundibuliforme y el espolón muy corto. Fotografías de Katya Romero.

Fenología. Se ha observado en floración y con hojas de verano en abril y mayo. Al parecer esta especie no forma rosetas de invierno, esto se deduce del hecho de que en las muestras examinadas no se encontraron evidencias de la existencia de hojas o rosetas de invierno, a pesar de que algunas fueron colectadas en el mes de abril.

Etimología. El nombre de la especie hace referencia a Honduras, el país de origen de las plantas.

Pinguicula hondurensis se ubica en el subgénero *Pinguicula* sección *Longitubus* Zamudio & Rzedowski, por la corola bilabiada, con el tubo largamente infundibuliforme, más largo que los lóbulos de la corola y el espolón muy corto; sin embargo, la condición homófila (solo con hojas de verano) y la corola morada de esta especie, son dos características novedosas para la sección, pues en la diagnosis original se estipula que las especies de este grupo son heterófilas, con hojas diferentes durante el verano y el invierno y tienen flores rojas (Casper 1962, 1966; Zamudio & Rzedowski 1991). Dentro de esta sección hasta ahora solo se conocían seis especies restringidas al territorio de la República Mexicana: *Pinguicula calderoniae* Zamudio, de los estados de Querétaro y San Luis Potosí, *P. crassifolia* Zamudio, de Hidalgo, *P. hemiepiphytica* Zamudio & Rzedowski, de Oaxaca, *P. laueana* Speta & Fuchs, de Oaxaca, *P. rzedowskiana* Zamudio & Juárez, de Querétaro, y *P. utricularioides* Zamudio & Rzedowski, de Oaxaca. (Speta & Fuchs 1989; Zamudio 1988; Zamudio 2001; Zamudio y Rzedowski 1991; Zamudio et al. 2018). La flor de la nueva especie es muy parecida a las de *Pinguicula utricularioides* y *P. rzedowskiana*, por el tubo largamente infundibuliforme y el espolón muy corto (Fig. 2B), pero difiere significativamente por la forma de las hojas (Fig. 2A) y por la ausencia de hojas de invierno. Las hojas de la nueva especie son parecidas a las hojas de verano de *Pinguicula hemiepiphytica*, pero esta última se diferencia por presentar do tipos de hojas durante el ciclo anual y por el tubo de la corola igual o más corto que el espolón.

La condición homófila y las flores moradas de *Pinguicula hondurensis* hacen necesario modificar la diagnosis de la sección para darle cabida, la que quedaría de la siguiente manera:

Sección *Longitubus* Zamudio & Rzed., Acta Bot. Mex. 14: 30–31. 1991 (emend. Zamudio).

Folia biformia vel uniformia hibernaculis nullis, corolla ringens, magna, profunde bilabiata rubra vel purpurea, labio infero quam supero majore lobis subaequalibus integerrimis vel emarginatis; tubus longe infundibuliformis; calcar rectum vel incurvatum tubum subaequans vel major vel minor.

Hojas dimórfas o isomórfas, hibernáculo ausente, corola grande, profundamente bilabiada, roja o morada, labio inferior más grande que el superior, lóbulos subiguales, enteros o emarginados, tubo largamente infundibuliformen, espolón recto o curvo, subigual, más corto o más largo que el tubo.

Pinguicula hondurensis es un elemento endémico de las montañas del centro y sureste de Honduras; así mismo, representa el extremo sur de la distribución geográfica de los miembros de la sección *Longitubus*. Es la única especie de este grupo registrada en Centroamérica, pues las demás se encuentran solo en las montañas mexicanas. Es importante resaltar que las especies de esta sección son endemismos estrechos, conocidas solo de una o dos localidades ubicadas en la cima de cerros muy altos o sistemas montañosos aislados, desde el centro de México hasta Honduras.

La siguiente clave permite distinguir las especies conocidas de *Pinguicula* sección *Longitubus.*

1. Plantas con flores moradas; con un solo tipo de hojas durante todo su ciclo (homófilas), originarias de Honduras ..... **Pinguicula hondurensis**
1. Plantas con flores rojas, violáceo-purpúreas o rosas; con dos tipos de hojas en rosetas subsecuentes durante un ciclo anual (heterófilas), originarias de México.

2. Plantas que florecen con la roseta de invierno.

3. Hojas de invierno espatuladas, hojas de verano induplicadas o sacciformes, pecioladas; plantas procedentes del cerro Pico Azul, Niltepec, Oaxaca ..... **Pinguicula utricularioides**
3. Hojas de invierno crasas, dolabriformes, elípticas a obovadas en contorno, hojas de verano obovadas, elípticas a oblongas.

4. Hojas de invierno dolabriformes a elípticas, formando una roseta laxa epigea, que semeja un maguey, hojas de verano elípticas a oblongas, pecioladas, flores rojo-purpúreas, plantas procedentes de El Chico, Hidalgo ..... **Pinguicula crassifolia**
4. Hojas de invierno ampliamente obovadas, hojas de verano obovadas, sin peciolo evidente, flores rojas, plantas procedentes de la Sierra Mixe, Oaxaca ..... **Pinguicula laueana**

2. Plantas que florecen con la roseta de verano.

5. Hojas de verano elípticas a circulares, hojas de invierno espatuladas a oblanceoladas; plantas procedentes de la Sierra de Juárez, Oaxaca ..... **Pinguicula hemiepiphytica**
5. Hojas de verano lineares o linear lanceoladas.

6. Tubo de la corola igual o más corto que el espolón, hojas de invierno crasas, obtruladas a elípticas, formando una roseta compacta hipogea; plantas conocidas de los municipios de Landa, Querétaro y Xilitla, San Luis Potosí ..... **Pinguicula calderoniae**
6. Tubo de la corola más largo que el espolón, hojas de invierno espatuladas a oblanceoladas, formando una roseta laxa, epigea; plantas conocidas del municipio de Landa, Querétaro ..... **Pinguicula rzedowskiana**

Es importante señalar que las plantas de *Pinguicula* no pueden ser identificadas sin flores, por lo que en la clave se usan los caracteres de las rosetas y hojas comúnmente presentes durante la floración, complementados con información de la forma de las hojas y rosetas alternas y de la distribución geográfica conocida.

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Los autores agradecemos a los curadores de los herbarios EAP, MEXU, MO por permitirnos revisar sus colecciones de Lentibulariaceae y por el préstamo de ejemplares para su estudio. A Jerzy Rzedowski por la revisión del manuscrito, a Andrés González por su ayuda en las exploraciones de campo, a Katya Romero por facilitarnos las fotografías, a Damián Piña por la preparación de la Figura 2 y a Manuel Ramírez por la elaboración de la ilustración.

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UNA ESPECIE NUEVA DE *PERYMENIUM* (COMPOSITAE) DEL CERRO TANCÍTARO, MICHOACÁN, MÉXICO

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RESUMEN

Se describe como especie nueva y se ilustra a **Perymenium garciaruizii** Rzed., **sp. nov.,** habitante del cerro Tancítaro, ubicado en el occidente de Michoacán. Se le relaciona con *P. alticola* McVaugh y con *P. berlandieri* DC. Se incluye un cuadro de características diferenciales entre los tres taxones.

ABSTRACT

Perymenium garciaruizii Rzed., **sp. nov.**, from Cerro Tancítaro in western Michoacán, Mexico, is described and illustrated. It is related to *P. alticola* McVaugh and to *P. berlandieri* DC. A table showing differences between these three taxa is included.

El estudio de materiales depositados en el herbario del Instituto de Ecología, A.C. en Pátzcuaro, Michoacán (IEB), ha revelado la existencia de la siguiente especie del género *Perymenium* (Compositae, Heliantheae) que se propone como nueva.

Perymenium garciaruizii Rzed. **sp. nov. TIPO**: **MÉXICO**. **Michoacán**. Mpio. Tancítaro: Cerro Tancítaro, 27 km al W de Uruapan en línea recta, peñas al NE del Cerro La Cruz, (102º20'50'' W, 19º24'00'' N), elev. 3020 m, arbusto de 1 a 1.5 m de alto, flores amarillas, en el bosque de coníferas, 26 Nov 1996, *I. García Ruiz 4466, c/J.A. Machuca y M. Cházaro* (holotipo: IEB; isotipo: CIMI). Figura 1.

Frutex 1–3 m altus; ramuli strigosi celeriter glabrescentes; folia petiolis 2–3 mm longis, laminis lanceolatis vel fere ovatis, (3)4–6.5 cm longis, 1.5–2.5 cm latis, apice acuminatis, base rotundatis vel truncatis, margine sparse denticulatis, triplinervatis vel trinervatis, subtus nervatione valde prominenti, utrinque strigosis et asperis, coriaceis, supra atroviridibus; capitula maximam partem in fasciculis terminalibus aggregata, pedicellis ad 2 cm longis; involucrum campanulatum 5–7 mm altum, phyllariis 12–16 aliquantum graduatis, externis saepe latioribus quam longioribus, interioribus ovatis ad lanceolatis, omnibus aliquantum reflexis; flores radii 3–5 fertiles, ligulis lineari-oblongis luteis ca. 8 mm longis; flores disci ca. 25 fertiles corollis tubularibus luteis ca. 6 mm longis glabris; achaenia oblonga concavo-convexa 2–2.5 mm longa brunnea, ad apicem hispidula, pappus 10–15 aristis tenuibus, maximam partem minus quam 2 mm longis, saepe etiam cum 1 vel 2 aristis ad 3.5 mm longis.

Arbusto de 1 a 3 m de alto; ramas teretes, café-grisáceas, ramillas estrigosas, muy pronto glabrescentes; hojas todas opuestas, peciolos de 2 a 3 mm de largo, láminas lanceoladas a casi ovadas, de (3)4 a 6.5 cm de largo y 1.5 a 2.5 cm de ancho, acuminadas y puntiagudas en el ápice, redondeadas a truncadas en la base, margen esparcidamente denticulado o rara vez casi entero, triplinervadas o a veces trinervadas, con venación muy prominente y reticulada en el envés, verdes muy oscuras en el haz, más claras en el envés, estrigosas y rasposas al tacto en ambas superficies, de textura coriácea; inflorescencias en forma de fascículos más o menos compactos ubicados en los extremos de las ramas, mayormente terminales y sésiles o casi sésiles y rodeados por las hojas subyacentes, a veces algunos también sobre pedúnculos hasta de 4 cm de largo, a partir de las axilas del siguiente nudo de hojas, pedicelos estrigosos, hasta de 2 cm de largo; involucro campanulado, de 5 a 6 mm de largo y casi otro tanto de diámetro, sus brácteas 12 a 16, dispuestas en 2 a 3 series de longitud desigual, las

exteriores a menudo más anchas que largas, de 3 a 4 mm de largo, las interiores ovadas a lanceoladas, todas agudas a obtusas y por lo común algo reflejas en el ápice, verdes, rígidas y coriáceas, estrigosas sobre todo hacia el ápice; páleas elípticas, conduplicadas, envolviendo las flores del disco, de ca. 5 mm de largo, acuminadas en el ápice, verdosas, glabras; flores del radio 3 a 5, fértiles, sus corolas de ca. 10 mm de largo, glabras, tubo de ca. 2 mm de largo, lígula linear-oblonga, de ca. 1.5 mm de ancho, ramas del estilo lineares, de ca. 1.5 mm de largo; flores del disco ca. 25, fértiles, sus corolas tubulosas, amarillas, de ca. 6 mm de largo, glabras, de los cuales ca. 1 mm corresponde a los lóbulos triangulares, papilosos por fuera; aquenios oblongos, cóncavo-convexos, de 2 a 2.5 mm de largo, cafés, hispídulos en la parte apical, vilano de 10 a 15 aristas delgadas, mayormente de poco menos de 2 mm de largo, a menudo también con una o dos hasta de 3.5 mm de largo, todas por lo general desprendiéndose con facilidad.

Material adicional examinado. MÉXICO. Michoacán. Mpio. Tancítaro: Cerro Tancítaro, 27 km al W de Uruapan en línea recta, La Laguna ca. de El Tepetate (102º15' W, 19º24'N), elev. 2900 m, arbusto de 2 a 3 m de alto, inflorescencia amarilla, creciendo en lugares sombreados de *Abies*, poco común, 29 Ago 1996, *I. García Ruiz 4137*, c/*J.A. Machuca* (CIMI, IEB).

Probablemente pertenece aquí asimismo otro espécimen del cerro Tancítaro: *Leavenworth & Hoogstraal 1208* (F, GH, MO, NY), colectado el 25 de julio de 1941 a la altitud de 9500 pies (ca. 2900 m), mencionado por Fye (1978, p. 272) como perteneciente a *Perymenium alticola* McVaugh.

Los dos ejemplares colectados por García Ruiz y colaboradores también fueron identificados inicialmente como *Perymenium alticola*, pero un examen comparativo con el isotipo de tal especie, procedente del estado de Jalisco, revela la existencia de varias distinciones significativas.

Perymenium alticola y *P. garciaruizii* comparten características de la pubescencia, de la forma de hojas, de involucros, flores y aquenios, así como de la afinidad ecológica, pues son habitantes de bosques de coníferas, en contraste con la mayoría de las especies de este género, que son propias de ambientes más calurosos o más secos.

La primera diferencia que llamó la atención es de carácter fenológico, pues las dos colectas conocidas de Jalisco fueron realizadas en marzo y abril, mientras que en el cerro Tancítaro las plantas se encontraron en flor entre julio y noviembre. Algunas discrepancias adicionales atañen el largo de los peciolos y de las láminas foliares, así como la forma de la inflorescencia, el tamaño de los involucros, la forma de sus brácteas, el número y largo de las flores del radio. El conjunto se detalla más en el Cuadro 1.

Por otro lado, es de trascendencia reconocer que el taxón nuevo debe estar relacionado también de cerca con *Perymenium berlandieri* DC., especie común en las montañas aledañas al Valle de México, conocida ya de numerosas colectas, desde la región limítrofe de Michoacán hasta el sector meridional de la Sierra Madre Oriental, en los estados de Hidalgo y Puebla. Esta última se distingue por su involucro más estrecho y más pronunciadamente graduado, pero en otros caracteres (incluyendo la afinidad ecológica) se asemeja bastante tanto a *P. alticola* (como ya lo ha sugerido Fay, op. cit.), como a *P. garciaruizii,* por lo que se le incluye en el mencionado cuadro.

Al parecer *Perymenium garciaruizii* es una especie estrechamente endémica, hasta ahora solo conocida de altitudes medianamente elevadas del cerro Tancítaro, montaña más alta del estado de Michoacán, ubicada en la parte occidental del mismo. Éste es un extenso macizo montañoso de origen volcánico, cuyo pico principal alcanza 4150 m s.n.m.

Es factible también la existencia de esta planta en el vecino y aun poco explorado cerro Patamban, ubicado unos 40 km más al norte, con altitud máxima cercana a 3500 m.

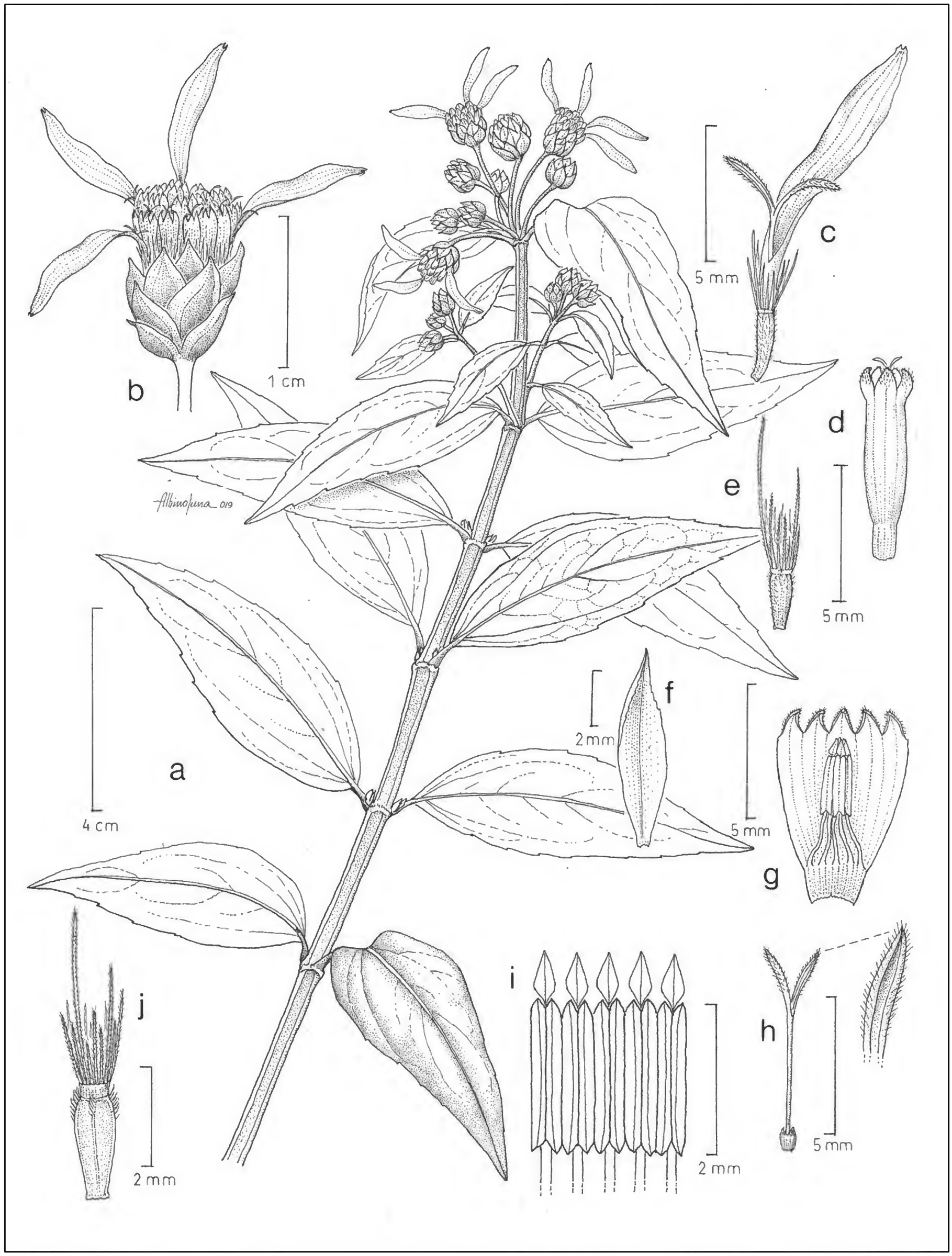

Figura 1. *Perymenium garciaruizii.* a. Rama con hojas e inflorescencia. b. Cabezuela. c. Flor del radio. d. Corola de la flor del disco. e. Aquenio de la flor del disco. f. Pálea. g. Corola de la flor del disco disecada, mostrando el androceo. h. Estilo de la flor del disco. i. Anteras. j. Aquenio maduro. Ilustrado por Albino Luna.

Caracteres	*P. alticola*	*P. berlandieri*	*P. garciaruizii*
Hojas			
largo del peciolo	3-25 mm	1-11(15) mm	2-3 mm
largo de la lámina	3-14 cm	1.5-13 cm	(3)4-6.5 cm
color del haz	verde olivo	verde oscuro	verde muy oscuro
textura	herbácea	herbácea	coriácea
venación del envés	prominente	prominente	sumamente prominente
Inflorescencias	abiertas	abiertas a compactas	compactas
pedicelos, largo	hasta de 6 cm	hasta de 7 cm	hasta de 2 cm
Involucros			
forma	campanulado a hemisférico	cilíndrico-campanulado	campanulado
largo	6.5-9 mm	5.5-8 mm	5-6 mm
ancho	4.5-7 mm	3.5-6.5 mm	4.5-5.5 mm
Brácteas del involucro			
disposición	levemente graduadas	notablemente graduadas	levemente graduadas
forma	ovadas a casi lineares	ovadas a oblongas	oblatas a lanceoladas
Flores del radio			
número	5-8	5-8	3-5
largo de lígula	10-20 mm	8-13 mm	±8 mm
Flores del disco			
largo de corola	6.5-9.5 mm	4-8 mm	±6 mm
Periodo de floración	marzo a abril	(julio) agosto a enero (febrero)	julio a noviembre
Distribución geográfica conocida	sur de Jalisco	este de Michoacán a Hidalgo, Morelos y Puebla	oeste de Michoacán

Cuadro 1. Principales características diferenciales entre *Perymenium alticola, P. berlandieri* y *P. garciaruizii.*

Perymenium alticola, P. berlandieri y *P. garciaruizii* son habitantes de tres áreas separadas a lo largo o cerca del Eje Volcánico Transversal de México. Dada su similitud morfológica y de tolerancias ecológicas, pueden considerarse como elementos vicariantes, probablemente procedentes de un antecesor común.

El nombre de la especie nueva se designa a Ignacio García Ruiz, colector de los dos ejemplares citados. Ignacio es un destacado botánico michoacano, fundador y curador del herbario CIMI, ubicado en la ciudad de Jiquilpan. En la última década del siglo pasado dedicó especial

esfuerzo a la exploración de la flora del cerro Tancítaro, que condujo a la publicación de un extenso catálogo (García Ruiz et al. 2002).

AGRADECIMIENTOS

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LECTOTIPIFICACIÓN DE NOMBRES EN ALGUNAS *MUHLENBERGIA* (POACEAE) DE MÉXICO

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ABSTRACT

As part of preparation of the taxonomic revision of the genus *Muhlenbergia* in the state of Guerrero, Mexico, lectotypes for five names are here designated: *M. alamosae* Vasey, *M. setarioides* E. Fourn., *Epicampes laxiuscula* E. Fourn., *Pereilema crinitum* J. Presl var. *cirratum* E. Fourn., and *P. ciliatum* E. Fourn.

RESUMEN

Como parte de la preparación de la revisión taxonómica del género *Muhlenbergia* para el estado de Guerrero, México, se designan aquí los lectotipos para cinco nombres: *M. alamosae* Vasey, *M. setarioides* E. Fourn., *Epicampes laxiuscula* E. Fourn., *Pereilema crinitum* J. Presl var. *cirratum* E. Fourn., y *P. ciliatum* E. Fourn.

El género *Muhlenbergia* Schreb. (Poaceae: Chloridoideae: Cynodonteae: Muhlenbergiinae) incluye aproximadamente 186 especies a nivel mundial (Soreng et al. 2017), la mayoría de ellas se distribuyen en el sur de los Estados Unidos de América y norte de México. *Muhlenbergia* es el mejor representado de las Poaceae en México, con aproximadamente 129 especies (Sánchez-Ken 2019). Las especies de *Muhlenbergia* son componentes de la vegetación primaria, ocupando hábitats como pastizales, bosques y matorrales, tanto en climas húmedos como en secos (Giraldo-Cañas & Peterson 2009). Además de su papel ecológico, el género es de importancia económica ya que numerosas especies son forrajeras y algunas como *M. dumosa* Scribn. ex Vasey y *M. macroura* (Kunth) Hitchc. tienen uso medicinal (Mejía-Saulés & Dávila 1992). Como parte de la preparación de la revisión taxonómica del género para el estado de Guerrero, México, se designan aquí los lectotipos para cinco nombres del género, de acuerdo con sugerencias en el Código Internacional de Nomenclatura Botánica (Turland et al. 2018).

MUHLENBERGIA ALAMOSAE Vasey, Bot. Gaz. 16: 146. 1891. **LECTOTIPO** (designado aquí): **MÉXICO. Sonora**. Sierra de los Álamos, 1890, *E. Palmer 407* (US00134299!; isolectotipos: ARIZ-BOT-0005386!, CAS0003592!, GH00024007!, K000308928!, MEXU00005189!, MICH1108711!, NY00381415!, US01164861!).

Comentarios—El ejemplar *E. Palmer 407* (US00134299) ha sido citado como el holotipo de *M. alamosae* por varios autores (Espejo et al. 2000; Peterson 2001; Herrera & Peterson 2007, 2017); sin embargo, en el protólogo (Vasey 1891) no se hace referencia a ningún herbario o lámina en particular. Vasey se encontraba adscrito a la Smithsonian Institution en el momento de la descripción de *M. alamosae* (Stafleu & Cowan 1986), por lo que con seguridad revisó el material depositado en el

herbario US. En dicha colección hay dos duplicados, uno de ellos etiquetado como holotipo (US00134299) y otro como isotipo (US01164861) por Paul M. Peterson en 1994. No se encontró evidencia de que Vasey haya empleado solamente una de las dos láminas para elaborar la descripción de *M. alamosae*, por lo que tanto los duplicados de US y como de otros herbarios deben de ser considerados como sintipos. En consecuencia, de acuerdo a Turland et al. (2018), se designa aquí como lectotipo la lámina *E. Palmer 407* (US00134299), que muestra las características importantes de la especie, mientras que los duplicados se consideran como isolectotipos.

MUHLENBERGIA GIGANTEA (E. Fourn.) Hitchc. in Britton, N. Amer. Fl. 17(6): 460. 1935. *Epicampes gigantea* E. Fourn., Mexic. Pl. 2: 88. 1886. **TIPO: MÉXICO. Veracruz**. Rio Blanco, prope Orizaba, Sep 1886, *E. Bourgeau 3137* (holotope: P; isotipos: G00099412!, MPU027109!, S14-29388!, US00433431!).

=*Epicampes bourgeaei* E. Fourn., Mexic. Pl. 2: 88. 1886. **TIPO: MÉXICO. Veracruz**. Escamela, prope Orizaba, Aug 1866. *E. Bourgeau 2973* (holotope: P; isotipos: K000308913!, US00433427!).

=*Epicampes bourgeaei* E. Fourn. var. *mutica* E. Fourn. Mexic. Pl. 2: 88. 1886. **LECTOTIPO** (designado por Herrera & Peterson 2007): **México**. **Veracruz**. El Mirador, 1841, *F.M. Liebmann 678* (holotope: US00133751!; isolectotipos: US 00133750!, K000308914).

=*Epicampes expansa* E. Fourn., Mexic. Pl. 2: 88. 1886. *Epicampes expansa* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 548. 1885, nom. nud. **TIPO: MÉXICO. Veracruz**. Orizaba, 1854, *M. Botteri 104* (holotope: P; isotipos: BM000938654!, US00433430!).

=*Epicampes laxiuscula* E. Fourn., Mexic. Pl. 2: 88. 1886. *Epicampes laxiuscula* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 549. 1885, nom. nud. **LECTOTIPO** (designado aquí): **MÉXICO**. **Veracruz**. Orizaba, Nov 1854, *M. Botteri 155* (BM000938656!; isolectotipo: US00433432!).

=*Epicampes ehrenbergii* Mez, Repert. Spec. Nov. Regni Veg. 17: 212. 1921. **TIPO: MÉXICO.** Cuesta de Pinoloco, s.f., *C. Ehrenberg 1156* (holotope: B; isotipo: US00433428!).

Comentarios—En el protólogo de *Epicampes laxiuscula* (Fournier 1886) se citan dos sintipos, uno de los cuales se elige aquí como lectotipo.

MUHLENBERGIA PEREILEMA P.M. Peterson, Caldasia 31: 293, f. 6 E-J. 2009. *Pereilema crinitum* J. Presl, in C. Presl, 1: 233, t. 37, f. a-f. 1830. **TIPO: PANAMÁ.** Habitat in Panama, s.f., *T. Haenke s.n.* (holotope: PR; isotipos: BR0000006886257!, MO123263!, MO123264!, W0029493!).

=*Pereilema setarioides* E. Fourn., Mexic. Pl. 2: 93. 1886. **TIPO: MÉXICO. Veracruz**. Orizaba, *Thomas* s.n. (holotope: P; isotipos: P00751688!, US00610878!).

=*Pereilema crinitum* J. Presl var. *cirratum* E. Fourn., Mexic. Pl. 2: 93. 1886. **LECTOTIPO** (designado aquí): **MÉXICO**. **Veracruz**. Orizaba, 24 Nov 1866, *E. Bourgeau 3272* (P00751681!; isolectotipos: S14-29644!, US001409301).

Comentarios—En el protólogo de *Pereilema crinitum* var. *cirratum* (Fournier, 1886) se citan once sintipos, uno de los cuales se elige aquí como lectotipo.

MUHLENBERGIA PLUMISETA Columbus, Aliso 28: 66. 2010. *Pereilema ciliatum* E. Fourn., Mexic. Pl. 2: 93. 1886. *Pereilema ciliatum* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 543. 1885, nom. nud. *Muhlenbergia plumosa* P.M. Peterson, Amer. J. Bot. 97: 1546. 2010, nom. illeg. superfl. **LECTOTIPO** (designado aquí): **MÉXICO**. **Veracruz**. Orizaba, 8 Dec 1865, *E. Bourgeau 3328* (P00751680!; isolectotipos: K000308948!, L0062312!, MPU026837!, S14-29646!).

Comentarios—En el protólogo de *Pereilema ciliatum* (Fournier 1886) se citan seis sintipos, uno de los cuales se elige aquí como lectotipo.

MUHLENBERGIA SETARIOIDES E. Fourn., Mexic. Pl. 2: 84. 1886. *Muhlenbergia setarioides* E. Fourn. ex Hemsl. Biol. Cent.-Amer., Bot. 3: 542. 1885. *Muhlenbergia sylvatica* (Torr.) Torr. ex A. Gray var. *setarioides* (E. Fourn.) Beal, Grass. N. Amer. 2: 249. 1896. **LECTOTIPO** (designado aquí): **MÉXICO**. **Veracruz**. Orizaba, 1866, *E. Bourgeau 3362* (K000308906!; isolectotipos: G00099164!, MO-105150!, MPU026952!, S14-29487!, US00610883!).

Comentarios—En el protólogo de *Muhlenbergia setarioides* (Fournier, 1886) se citan siete sintipos, uno de los cuales se elige aquí como lectotipo.

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STOKESIA LAEVIS (ASTERACEAE), A NATIVE OF THE TEXAS FLORA

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ABSTRACT

Stokesia laevis is reported as new to the native flora of Texas based on a collection from a baygall forest of northern Jasper County. The population is disjunct there from its nearest known occurrence in western Louisiana. A list of species associated with *Stokesia* and a list of noteworthy species for the area (rare for Texas) are provided.

Stokesia laevis (Hill) Greene is not included in the Manual of the Vascular Plants of Texas (Correll & Johnston 1970), Atlas of the Vascular Plants of Texas (Turner et al. 2003), Plants Database (USDA, NRCS 2019), Biota of North America Program (Kartez 2019), or Flora of North America North of Mexico (Strother 2006). We report the species as a member of the native flora, based on the following specimen.

Voucher. **Texas**. Jasper Co.: 0.4 mi ESE of the junction of FS Rd 352 and FS RD 352A on W side of Trout Creek, second west fork S of the head of Trout Creek, baygall and moderately seepy seepage slopes along drainageways between sandhill ridges and on banks of small perennial side stream flowing into the main stem of Trout Creek, Angelina National Forest, 31° 4'40.88" N, 94° 11'44.17" W, 4 Sep 2019, *Singhurst*, *Philipps*, *Loos*, *Keith*, & *Buckingham 22,272* (BAYLU, TEX). Figures 1-3.

Figure 1. *Stokesia laevis* in Jasper Co., Texas. Photo by Jason Singhurst, 4 September 2019.

Figure 2. *Stokesia laevis* in fruit, Jasper Co. Texas. Photo by Jason Singhurst, 4 September 2019.

Stokesia laevis is native to Alabama, Florida, Georgia, Louisiana, Mississippi, and South Carolina of the southeastern USA and is introduced in North Carolina (Kartesz 2019). The Texas location is approximately 80 km (50 miles) from the nearest eastern location in Sabine Par., Louisiana (Kartesz 2019). Throughout its range, the species occurs in pitcher plant bogs, seeps, low pine woodlands, and wet ditches, as well a wider range of soil and moisture conditions.

The species was discovered by Peter Loos on 16 August 2019 during a botanical survey of the Trout Creek watershed in the Angelina National Forest. The plants grow on moderately wet seepage slopes along drainageways between sandhill ridges and on banks of a small perennial side stream that flows into main stem of Trout Creek. They were photographed by Loos on 16 August 2019 and identified by regional botanists as *Stokesia laevis*. The population was surveyed on 4 September 2019. Forty-three plants were observed in an area less than 1000 m^2 — 21 had maturing fruit and 22 were rosettes of varying size.

The location is a baygall (seepage forest) within an intact mature longleaf pine (*Pinus palustris*) upland. Common associated species include *Magnolia virginiana*, *Nyssa biflora*, *Quercus laurifolia*, *Cyrilla racemiflora*, *Rhododendron oblongifolium*, *Viburnum nudum*, *Persea palustris*, *Lyonia ligustrina*, *Myrica heterophylla*, *Vaccinium corymbosum*, *Toxicodendron vernix*, *Osmunda regalis*, *Osmunda cinnamomea*, *Smilax walteri*, *Sphagnum* sp., and numerous sedges (Cyperaceae). A population of the globally rare roughstem coneflower (*Rudbeckia scabrifolia*) was present as well as other characteristic baygall flora, including *Coreopsis tripteris*, *Doellingeria sericocarpoides*, *Eleocharis tuberculosa*, *Eupatorium perfoliatum*, *Oxypolis rigidior*, *Platanthera ciliaris*, and *Woodwardia areolata*.

Figure 3. Baygall forest habitat of *Stokesia laevis* in Jasper Co., Texas. Photo by Jason Singhurst, 4 September 2019.

This region of Texas occurs at the western edge of the Gulf coastal plain and contains a unique assemblage of rich woods, bog, and baygall species considered rare in the state. Noteworthy peripheral species in this region (southern Angelina and Sabine counties and northern Jasper and Newton counties) include *Amelanchier arborea*, *Bartonia paniculata* var. *texana*, *Calycocarpum lyonii*, *Cornus alternifolia*, *Houstonia purpurea*, *Lyonia lucida*, *Magnolia pyramidata*, *Phlox divaricata, Platanthera integra, Prenanthes barbata*, *P. altissima*, *Rudbeckia laciniata*, *Stewartia malacodendron*, *Trillium ludovicianum*, *Verbesina walteri*, and *Xanthorhiza simplicissima*, among others. *Stokesia laevis* may be added to the rare plant list.

ACKNOWLEDGEMENTS

We are indebted to United States Forest Service for providing access to this population, managing this unique landscape with their prescribed burning program, and the potential opportunity to locate additional *Stokesia laevis* plants in the baygall habitats of the Angelina National Forest. This study and report result from cooperation between federal, state, and local agencies, as cited in the affiliations of the authors.

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STUDIES OF NEOTROPICAL COMPOSITAE–XIII. *LAGASCEA ESPINALII* (HELIANTHEAE: HELIANTHINAE), A NEW SPECIES FROM DRY CANYONS IN ANTIOQUIA, COLOMBIA, AND TWO NOTEWORTHY RANGE EXTENSIONS

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ABSTRACT

The uniflorous-capitulate new species **Lagascea espinalii** Pruski, **sp. nov.** is described, and is endemic to dry canyons in the Cauca river basin in Antioquia, Colombia. *Lagascea espinalii* (Heliantheae) is placed in *Lagascea* sect. *Nocca*, and compared to its congeners. *Lagascea espinalii* is the ninth species recognized in the genus, the second species of the genus known in South America, and the first species of *Lagascea* sect. *Nocca* reported in South America. A key to species of *Lagascea* is given. Additionally, noteworthy range extensions reported here include the first report of the genus *Florestina* (*F. latifolia*) (Bahieae) in South America and the first report of the genus *Gongylolepis* (*G. colombiana*) (Mutisieae s.l.) in Antioquia, Colombia.

Herbarium studies in Colombia have resulted in the present description of a new species of the paucispeciose, western Mexico-centered, uniflorous-capitulate genus *Lagascea* Cav. (Heliantheae: Helianthinae). The new species, shrubby, white-flowered *Lagascea espinalii* Pruski, occurs in seasonally dry forested (bosque seco tropical) canyons and bordering premontane areas of the inter-Andean Cauca River basin in Antioquia, Colombia. *Lagascea espinalii* is partly sympatric with the similarly-scurfy, regional *Simsia fruticulosa* (Spreng.) S.F. Blake (Helianthinae) and the well-known *L. mollis* Cav. (Fig. 1A). Vegetative portions of *L. espinalii* resemble in gestalt Mexican-Central American *Tithonia longiradiata* (Bertol.) S.F. Blake (Helianthinae), and perhaps tellingly *Lagascea* and *Tithonia* Desf. ex Juss. were given as sister genera by Schilling and Panero (2011).

The relations of *Lagascea* were discussed and the genus revised by Stuessy (1976, 1978), who recognized eight species in three sections. Stuessy (1978) recognized two species in diffusely branched, herbaceous, minutely coroniform-fruited *Lagascea* sect. *Lagascea* (Fig. 1A); two shrubby species with golden-yellow corollas and an often rudimentary pappus in *Lagascea* sect. *Calhounia* (A. Nels.) Stuessy (Fig. 1B); and four (now five) shrubby species with white (-pinkish) corollas and a biaristate pappus within *Lagascea* sect. *Nocca* (Cav.) DC. (Fig. 1C).

The genus *Lagascea* is characterized traditionally as being (secondarily) uniflorous-capitulate, with the single floret surrounded proximally by a thin, gamophyllous, tubular-dentate, calyx-like true involucre (Figs. 2–3, 7–8; viz also Hind et al. 1993: pl. 64). In interpreting the capitula as monocephalous, Brown (1817) noted the significance of the ovary as free from (rather than adnate to) the surrounding gamophyllous involucre, as is typical of ovaries in pluriflorous-capitulate Compositae. These epaleate, uniflorous capitula of *Lagascea* are sessile and aggregated onto a shared base of a larger, pluricapitulate, (tertiary) compound glomerate-synflorescence (Stuessy 1978; Harris 1994; Medabalimi & Aluri 2017; Pruski & Robinson 2018). Each pluricapitulate synflorescence (aka compound head, syncephalum, etc.) is in turn usually subtended by a leafy-paucibracteate, false secondary involucre (Figs. 4–7). The synflorescences of *Lagascea* are either grouped terminally on branchlets (Figs. 1A, 1C, 4–5), or on occasion (e.g., *Lagascea* sect. *Calhounia*) they occur singly (Figs. 1B, 2B).

The interpretation of the capitula as typically uniflorous is further supported by Hemsley (1881) and Stuessy (1978), who noted the occasional occurrence of 2–5(–8) florets in *Lagascea decipiens* (Fig. 2A right; viz also *Parkinson s.n.*, the type of synonymous *L. biflora* Hemsley) within the calyx-like involucre of some individual capitula. In instances when > 3-flowered, Stuessy gave capitula as often weakly paleate, with involucres and paleae developmentally and structurally distinct. Species of the genus *Lagascea* may often be recognized without dissection by the basically eximbricate (never spirally gradually-imbricated), leafy-bracteate, false involucre of their synflorescences (Figs. 4–7), and by the characteristic sericeous-pilose indument of their involucres, stems, and/or leaves.

The synflorescences of the genus *Lagascea* (Figs. 1–2, 4–7) functionally mimic pluriflorous capitula of archetypal Compositae (viz Cavanilles 1794, 1803; Jacquin 1809; Brown 1817; Kunth 1820; Cassini 1828; Lessing 1832; Candolle 1836; Endlicher 1836–1840; Spach 1841; Gardner 1846; Walpers 1846–1847; Schultz-Bipontinus 1861). The aforementioned early authors mostly treated uniflorous-capitulate *Lagascea* as tribe Vernonieae near monotypic and uniflorous-capitulate *Rolandra* Rottb. and *Spiracantha* Kunth. *Lagascea* superficially resembles tribe Vernonieae by its linear-lanceolate, long-papillose style branches with continuous stigmatic surfaces. Although *Lagascea* and Vernonieae have vaguely similar style branches, the smooth-glabrous style trunk, recurved style branches, and carbonized cypselae of *Lagascea* are obviously at odds with a placement in Vernonieae. Uniflorous-capitulate *Lagascea* was treated subsequently as a member of tribe Heliantheae (e.g., Bentham & Hooker 1873; Clarke 1876; Hemsley 1881; Hooker 1881; Baillon 1882; Baker 1884; Hoffmann 1894), where it still remains.

The uniflorous capitula of *Coulterella* Vasey & Rose lead these authors to suggest a placement of the genus in subtribe Lagasceinae, but Stuessy (1976) distanced *Lagascea* and *Coulterella*, and "abandoned" Lagasceinae. Stuessy (1976) gave *Coulterella* as closest to *Flaveria* Juss. (both are now placed in tribe Tageteae; Panero 2007). Stuessy (1976) placed *Lagascea* in subtribe Helianthinae as "at least somewhat close" to *Alvordia* Brandegee, which was reduced to synonymy with *Aldama* La Llave (Helianthinae) by Schilling and Panero (2011). *Aldama dentata* La Llave and *Sclerocarpus* Jacq. (Helianthinae), by their disk cypselae held within paleae in perigynia-like structures, are superficially similar to *Lagascea*, but differ obviously by their pluriflorous, radiate capitula. Brandegee (1899, sub *Alvordia*) characterized the capitula of *Aldama fruticosa* (Brandegee) E.E. Schill. & Panero as uniflorous-capitulate, and Schilling and Panero (2011) highlighted the trend to few-flowered capitula in this and several other Helianthinae. Stuessy (1976) stated that although *Alvordia fruticosa* Brandegee is "almost secondarily headed," it lacks the "common secondary involucre" of *Lagascea.*

Elsewhere in Heliantheae, pistillate capitula of wind-pollinated *Ambrosia* L. (subtribe Ambrosiinae) are also characteristically uniflorous-capitulate. Pistillate capitula of *Xanthium* L. (subtribe Ambrosiinae) are 2-flowered. In these two Ambrosiinae genera, the florets of the pistillate capitula are extremely reduced and lack corollas. Nearly as reduced are the often 2-flowered capitula of *Delilia biflora* (L.) Kuntze and *Stachycephalum asplundii* H. Rob. & Tangerini, each Heliantheae. Nevertheless, *Lagascea* is equally odd, and is the sole primarily uniflorous-capitulate (Figs. 2–3, 7–8), syncephalous (Figs. 1–2, 4–7) genus of Heliantheae, a tribe of 100+ genera and about 1500 species, more or less 0.5 % of the Angiosperms (Panero 2007; Pruski & Robinson 2018). The circumscription of subtribe Helianthinae and the component genera recognized basically follows the treatments of H. Robinson (1981), Schilling and Panero (2002, 2011), Panero (2007), and Pruski and Robinson (2018). Schilling and Panero (2011) gave the singular *Lagascea* as late divergent in Helianthinae. Although flower color varies (Fig. 1), the gamophyllous phyllaries, uniflorous capitula, and stipitate glands of the branches help define *Lagascea*.

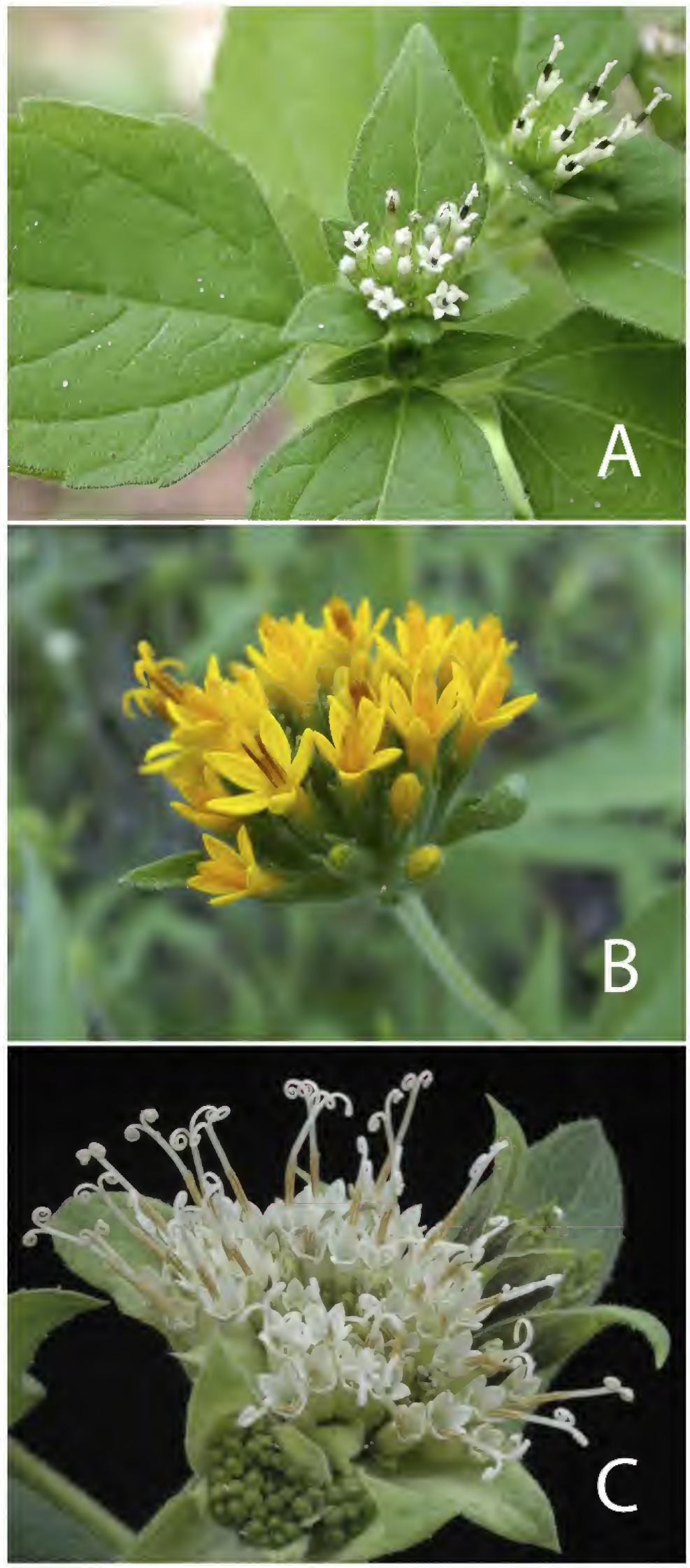

Figure 1. Glomerate-synflorescences of the three sections of *Lagascea*. A. Herbaceous *Lagascea mollis* of sect. *Lagascea*, with white corollas and black anthers. B. Shrubby *Lagascea decipiens* of sect. *Calhounia*, showing golden-yellow corollas. C. Shrubby *Lagascea helianthifolia* of sect. *Nocca*, with white corollas, brownish-anthers, and several clustered synflorescences (a compound head of compound heads, so to speak). (A *John Hayden 4711*, Yucatán, Mexico; B *Susan Carnahan 1959*, Arizona, USA; C *Pedro Tenorio Lezama s.n.,* same species as *Pedro Tenorio Lezama 21374*, Oaxaca, Mexico; photographs by the collectors).

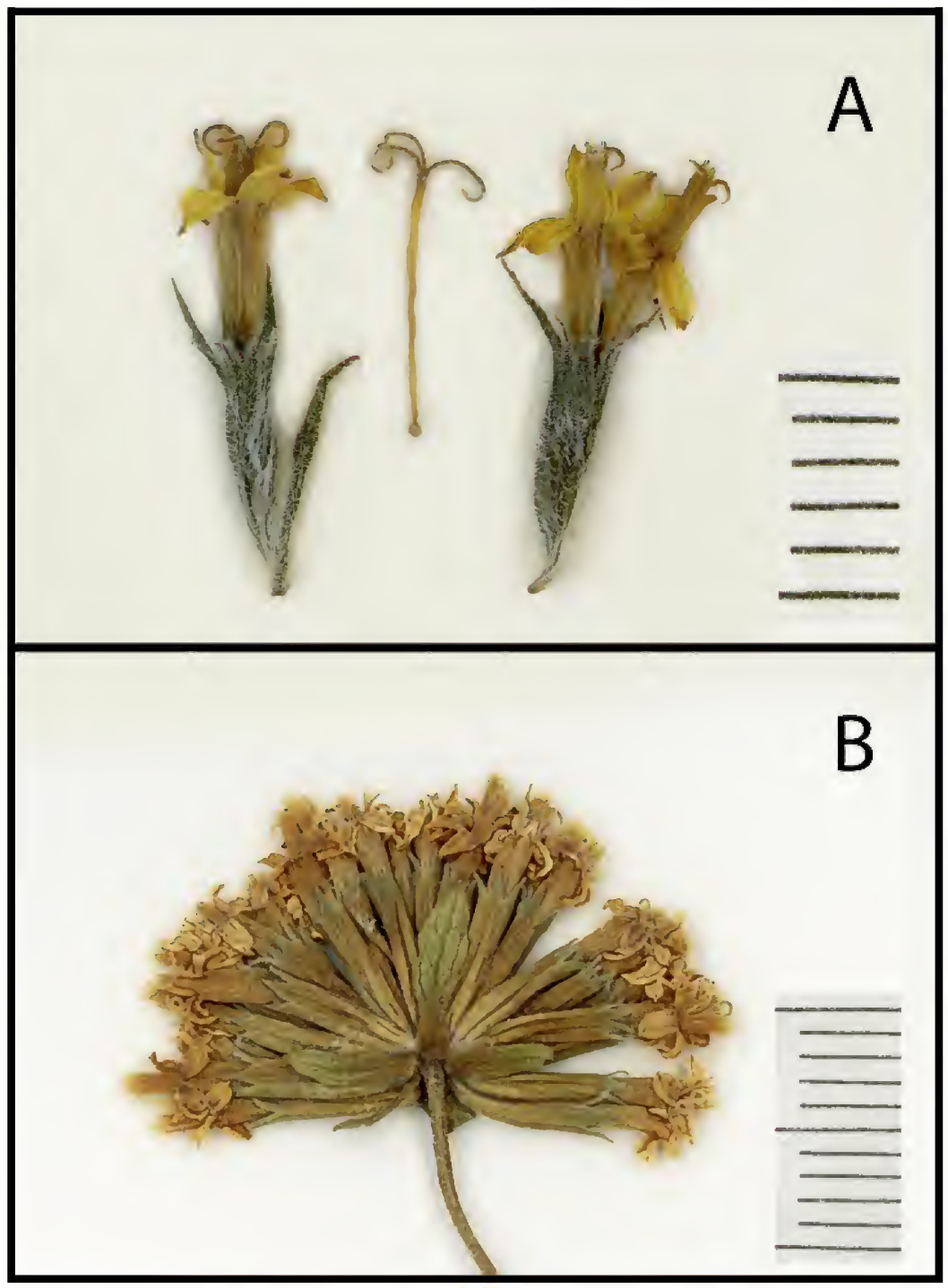

Figure 2. Capitula and synflorescence of *Lagascea* sect. *Calhounia*. A. Capitula (left, uniflorous; right, biflorous) and aberrant trifid style (center) of *L. decipiens*. B. Synflorescence of *L. palmeri*, showing the individual component capitula between narrow synflorescence bracts. (A *Sanders et al. 12935*, MO; B *García & Delgado 931*, MO). Metric scales lower right.

Important early summaries of *Lagascea* were given by Candolle (1836), Hemsley (1881), and B.L. Robinson (1901, 1907). Stuessy (1978) recognized a few infraspecies using the character of stipitate-glands on branchlets subtending the synflorescences. *Lagascea espinalii* typically has distal branchlets obviously stipitate-glandular (e.g., holotype, Fig. 5), albeit some more-proximal branchlets with budding flowers (e.g., paratype, Fig. 4) are not obviously glandular. Because the very striking stipitate glands are not always obviously manifest on the clearly conspecific material examined of *L. espinalii*, this character is not used by me as important in infraspecies taxonomy.

Of the eight species of *Lagascea* recognized by Stuessy (1978), only herbaceous *L. mollis* Cav. (Fig. 1A) (the generitype) was given formerly as occurring in South America. *Lagascea mollis* is found in Mexico, Central America, the West Indies, South America, and has also been reported as introduced sporadically in the Paleotropics (e.g., Africa, Asia, and Pacific Islands) (viz treatments by Kunth 1820; Candolle 1836; Bentham & Hooker 1873; Clarke 1876; Hooker 1881; Baker 1884; B.L. Robinson 1901, 1907; Liogier 1962, 1996, 1997; Aristeguieta 1964; Adams 1972; Clewell 1975; Nash & Williams 1976; Cabrera 1978; Stuessy 1978; Howard 1979; Grierson 1980; H. Robinson 1981, 2006; McVaugh 1984; Villaseñor 1989; Smith & Carr 1991; Hind et al.1993; Badillo 1994; Bremer 1994; Chowdhery 1995; Funk & Pruski 1996; Pruski 1997; Strother 1999; Dillon et al. 2001; Beentje et al. 2005; Barkley et al. 2006; Panero 2007; Chen & Hind 2011; Pruski & Funston 2011;

Rzedowski et al. 2011; Freire 2015; Turner 2015; Koyama et al. 2016; Pruski & Robinson 2018). The second of two species of herbaceous *Lagascea* sect. *Lagascea* is *L. aurea* Stuessy, a Mexican endemic with yellow corollas. Both species have main nerves of the involucre with several small resinous glands, which are especially prominent in fruit. *Lagascea* sect. *Lagascea* is in turn the sole section known previously to occur in South America.

Stuessy (1978) treated the two shrubby species [*Lagascea decipiens* Hemsl. and *L. palmeri* (B.L. Rob.) B.L. Rob.] having florets with short-tubed, golden-yellow corollas and usually one elongate gland in the main nerve of each involucral lobe (phyllary) as comprising the ditypic *Lagascea* sect. *Calhounia*. *Lagascea decipiens* (Figs. 1B, 2A) and *L. palmeri* (Fig. 2B) are each typified by material from Mexico, with *L. decipiens* also extending northward into the United States. *Lagascea* sect. *Calhounia* is not known from Central America (Stuessy 1978; Pruski & Robinson 2018), and thereby seems unlikely to occur in South America.

The four remaining species of *Lagascea* [*L. angustifolia* DC., *L. helianthifolia* Kunth, *L. heteropappa* Hemsl., and *L. rigida* (Cav.) Stuessy] are each typified by Mexican material, and were treated by Robinson (1901) as *Nocca* Cav. Stuessy (1978) recognized them as *Lagascea* sect. *Nocca*, which he characterized as having a shrubby habit, white (-pinkish) corollas, usually two–few elongate glands in the main nerve of each involucral lobe (phyllary), and a biaristate pappus. Plants determined here as *L. espinalii* are shrubs, have white corollas, and are biaristate-pappose. It is thus within *Lagascea* sect. *Nocca* that I describe *L. espinalii*, although the plants are without obvious elongate glands in the main nerve of each phyllary (involucral lobe).

Among the four species of this section recognized by Stuessy (1978), *Lagascea espinalii* is least dissimilar to Mexican-Central American (Mexico, Guatemala, Honduras, El Salvador, and Nicaragua) *L. helianthifolia* (Figs. 1C, 6–8), with the two species being superficially alike in their relatively long leaves that are usually obviously trinerved. *Lagascea espinalii* differs from *L. helianthifolia* by always alternate (vs. usually opposite to sometimes alternate) flowering branch leaves; by petiolate and smooth-surfaced (vs. either subsessile or reticulate-veined) leaves; by leaf blades 3-nerved from near (vs. 3-nerved from well-above) base; by sometimes purplish (vs. green) synflorescence bracts; by corollas 8–9.9 (vs. 10.5–17) mm long with tube 1.1–1.5 (vs. 2–4) mm long and about 3–4 (vs. 1–2) times shorter than corolla throat (viz Fig. 3 vs. Figs. 7–8); by style branches weakly (vs. well-) exserted from anther cylinder (viz Fig. 3 vs. Figs. 6–7); by immature cypselae 3.5–4 (vs. mature cypselae 5–7) mm long; and by pappus aristae 0.5–1.3 (vs. 0.4–0.5) mm long with the longer of the two about as long as (vs. shorter than) the short corolla tube (viz Fig. 3 vs. Fig. 8). *Lagascea espinalii* and *L. helianthifolia* are fairly disparate morphologically, and disjunct by about 1400 kms.

The three other species of *Lagascea* sect. *Nocca*—*L. angustifolia*, *L. heteropappa*, and *L. rigida* — are Mexican endemics and mutually similar by leaves always opposite throughout, short petioles, leaf blade size, leaf blade shape, and lack of long-narrow leaf blade tips. These three species thereby stand apart from *L. espinalii* and *L. helianthifolia*. *Lagascea rigida* has suprabasal leaf blade trinervy, which is also hinted at in *L. angustifolia* and *L. heteropappa*. *Lagascea heteropappa* by its strongly discolorous leaves with abaxial sericeous indument is somewhat similar to *L. espinalii*. *Lagascea heteropappa* clearly differs from *L. espinalii*, however, by its opposite (vs. alternate) flowering branch leaves, and nitidous (vs. dull-green) adaxial leaf blade surfaces. *Lagascea angustifolia* and *L. rigida* are very distinct from *L. espinalii*, and distinguished, respectively, by broad-acute–obtuse-tipped leaves or by adaxially nitidous, subglabrous leaves. The four species in the two other sections of *Lagascea* are either shrubs with golden-yellow corollas or are diffuse herbs, thus differing from *L. espinalii*. *Lagascea espinalii* can be inserted into the Stuessy (1978: 89) key before lead d. A key to species of *Lagascea*, modifying Stuessy (1978) and Turner (2015), is given below.

Figure 3. *Lagascea espinalii,* floral dissections of uniflorous capitula arranged following protologue figures of *Lagascea mollis* Cavanilles 1803: tab. 44 and *Lagascea rubra* Kunth 1820: tab. 311. A. Dissected synflorescence showing stipitate-glandular branchlet (bottom center), one bract (upper left), and a single capitulum (upper right). B. Unequally 5-lobed involucre, floret removed. C. Capitulum. D. Gamophyllous involucre (left) with floret removed and on right, showing immature biaristate cypsela with longer arista nearly as long as corolla tube. (A–B holotype, *Zapata 2147*, JAUM; C–D paratype, *Zapata 2148*, JAUM). Scale bars 5 mm.

Figure 4. *Lagascea espinalii*, portion of branch showing alternate leaves, blades trinerved from near base, long-narrow leaf blade tips, and axillary branchlets terminated by several pre-anthesis, leafy-bracteate synflorescences. (Paratype, *Zapata 2148*, sheet 1 of 2, JAUM).

Lagascea espinalii is the only species of *Lagascea* not occurring in Mexico, and is the sole species of *Lagascea* endemic to Colombia. *Lagascea espinalii* is the first species of *Lagascea* sect. *Nocca* reported in South America, and the second species of the genus known in South America. Similarly, only two species of *Lagascea* are known in Central America (Stuessy 1978; Pruski & Robinson 2018). The description of *L. espinalii* raises to nine the number of species of *Lagascea*, and to five the number of species now recognized in *Lagascea* sect. *Nocca*. It is quite natural to suggest that *L. espinalii* may be derived from congeners of Mexico-Central America, the center of distribution of *Lagascea* sect. *Nocca*.

LAGASCEA ESPINALII Pruski, **sp. nov.** **TYPE: COLOMBIA. Antioquia.** Mpio. Santa Fe de Antioquia, sector La Chorquina, vía a Urabá 10 km antes de Cativo, Bs-T, transición, vegetación secundaria, 1253 m, 5 Nov 2018, *Diego Zapata 2147* (holotype: JAUM-82165, as 2147 (1/2); isotype: JUAM-82166, as 2147 (2/2)). I annotated the holotype and isotype in JAUM as paratypes of a non-published name in *Lagascea* that used 'velezii' as the epithet. Figures 3–5.

Plantae fruticosae 1.5–2.5 m altae; ramuli sericeo-pilosi distaliter stipitato-glandulosi; folia 7–22 cm longa simplicia alterna petiolata, lamina (6.5–)9–19 × 3–8 cm lanceolata vel ovata 3-nervata basi cuneata integra apice acuminata vel longiattenuata supra brevisericea subtus longisericea, petiolo 0.5–3 cm longo; capitulescentia terminalis cymosa; synflorescentia 1.5–2.2 × 1.5–2.5 cm, campanulata 13+-capitulata bracteata, bracteas 5–6, 15–27 × 3–7 mm; capitula uniflora homogama discoidea 16–19 mm

longa epaleacea, involucrum 7–10 mm longum gamophyllum anguste obconicum quinquelobatum; flosculi disci 1 hermaphroditi 16–19 mm longis, corollis 8–9.9 mm longis infundibuliformis albis sericeo-pilosis tubo 1.1–1.5 mm longo lobis 1.8–2.3 mm longis; antherae 4–4.4 mm longae; styli rami circiter 1.5 mm longi; cypselae 3.5–4 mm longae biaristatae.

Monecious shrubs 1.5–2.5 m tall, woody-based with short main trunk, but with herbaceous flowering stems probably produced annually, without secretory cavities or latex; stems ascending, typically alternately several-many-branched from near mid-stem, leafy, flowering branchlets to ca. 1 m long, leafy, unbranched or few-branched only proximally, subdistal internodes shorter than leaves, brown, sericeous-pilose or hirsute to densely so, the pale-griseous trichomes often to 3+ mm long, branchlets subtending glomerules distally becoming mixed with long-stipitate-glandular indument often to 0.5+ mm long, sometimes the stipitate-glands nearly replace the sericeous-pilose trichomes. **Leaves** 7–22 cm long, simple, alternate for most of the length of the 10+ flowering stems, but leaves of young plants or proximal leaves opposite, petiolate; blade (6.5–)9–19 × 3–8 cm, mostly lanceolate to ovate, stiffly chartaceous, venation arching 3-nerved from acumination near base, this proximal pair of veins usually slightly thicker and more prominent than spreading distal secondaries, the larger distal secondary veins sometimes unequally thickened, more or less evenly spaced and arching towards apex, base tapering cuneate, margins unlobed, subentire, apex acuminate to long-attenuate or even nearly caudate, surfaces concolorous or slightly discolorous, eglandular, adaxial surface short-sericeous, dull-green, abaxial surface long-sericeous, pale green; petiole 0.5–3 cm long, short and broad in immature plants, but ultimately distinct and narrowly winged distally from decurrent blade, pilose, trichomes to 4+ mm long and sometimes longer than petiole width. **Capitulescence** terminal and also on alternate branchlets one per node from distal nodes, the terminal portion to 30 cm long, few–several-branched, usually leafless, 25+-capitulate, the proximal axillary flowering branchlets with about 3–6 loosely-arranged cymose shortly stalked (mostly 0.5–1.5 cm long) synflorescences, unbranched in proximal 1/2–2/3, few-bracteolate, axillary branchlets usually 10–15 cm long and shorter than subtending leaves, all branches loosely pilose with trichomes to 5 mm long, trichomes often longer than branch diameter, distal branchlets subtending glomerules often also stipitate-glandular. **Synflorescences** mimicking a pluriflorous capitulum, each with 13+, aggregated-glomerate, sessile, free, uniflorous capitula, 1.5–2.2 × 1.5–2.5 cm, campanulate, subtended by a false involucre of leafy bracts, individual synflorescences loosely cymose at ends of distal branchlets; leafy bracts of false involucre mostly 5–6, 15–27 × 3–7 mm, mostly lanceolate to oblong, green or purplish, effectively eximbricate, weakly overlapping at anthesis but pressing as thought loosely arranged, ascending to spreading, often trinerved from near base, apex acute, sericeous-pilose; branchlets subtending synflorescence mostly 0.5–1.5 cm long, sericeous-pilose and characteristically also densely stipitate-glandular, the stipitate-glandular indument sometimes becoming brownish or golden and partly obscuring the sericeous-pilose indument. **Capitula** uniflorous, homogamous, discoid, 16–19 mm long from base to tip of anthers, sessile on shared glomerule base; involucre 7–10 mm long, gamophyllous to near apex, narrowly-obconic, surrounding and enclosing the shorter cypsela, long-sericeous-pilose throughout but more densely so proximally, thin-scarious-chartaceous, the pale greenish surfaces nearly obscured by indumentum, trichomes to 1.3+ mm long, ca. 10-nerved, nerves brownish, the central nerve of each lobe (phyllary) thicker than laterals, slightly resinous-glandular, lobes 5, unequal or sometimes subequal, 1.5–3 mm long, linear-lanceolate, erect or spreading, attenuate-tipped; phyllaries connate for most of their length into an involucral tube with free apical lobes, thus effectively eximbricate and 1-seriate, persistent; clinanthium minute, epaleate. **Ray florets** 0. **Disk florets** 1, bisexual, 16–19 mm long from base to tip of anthers, exserted from involucre for about 1/3–1/2 their length, corolla tube and base of corolla throat held within involucre; corolla 8–9.9 mm long, reaching to about top of synflorescence bracts, funnelform, shortly 5-lobed, white (cream-colored), loosely short-sericeous-pilose proximally, grading to moderately long-sericeous-pilose distally, trichomes mostly 0.2–0.7 mm long, tube 1.1–1.5 mm long, about 3–4 times shorter than corolla throat, limb slightly broadened, throat 5.1–6.1 mm long, without prominent fibers associated with the five nerves, nerves proximally alternating with lobes, divaricate at sinuses and passing laterally into adjacent lobes, lobes 1.8–2.3 mm long, ascending to slightly recurved, nerves intramarginal and confluent distally forming a closed loop; anthers 4–4.4 mm long, mostly exserted from corolla, ecaudate, short-sagittate, filaments glabrous, thecae pale yellow-brown, connective darkish, sericeous in

distal half, appendages 0.5–0.7 mm long, long triangular, concave-navicular, eglandular, without resin ducts, partly obscured proximally by elongate connective trichomes but apparently not sericeous; endothecial pattern polarized; pollen spheroidal, tricolporate, echinate; styles base short-nodular, trunk smooth and glabrous, branches ca. 1.5 mm long, linear-lanceolate, white, only weakly exserted from anther cylinder in herbarium material seen, slightly recurved, abaxially obviously long-papillose, stigmatic surfaces of each branch continuous to near apex, not at all obviously 2-banded, apex narrowly tapered. **Cypselae** (immature) 3.5–4 mm long, obovoid, free from the gamophyllous involucre, rounded apically and tapered proximally, black, carbonized with phytomelanin deposits, without raphid crystals, smooth and not at all tuberculate, exalate, glabrous or nearly so, carpopodium small and nearly obscure; pappus low coroniform and laterally biaristate, aristae 0.5–1.3 mm long, slightly unequal, crown 0.3–0.4 mm long. Chromosome number unknown, base number presumably $x = 17$, as in related (all diploid) species.

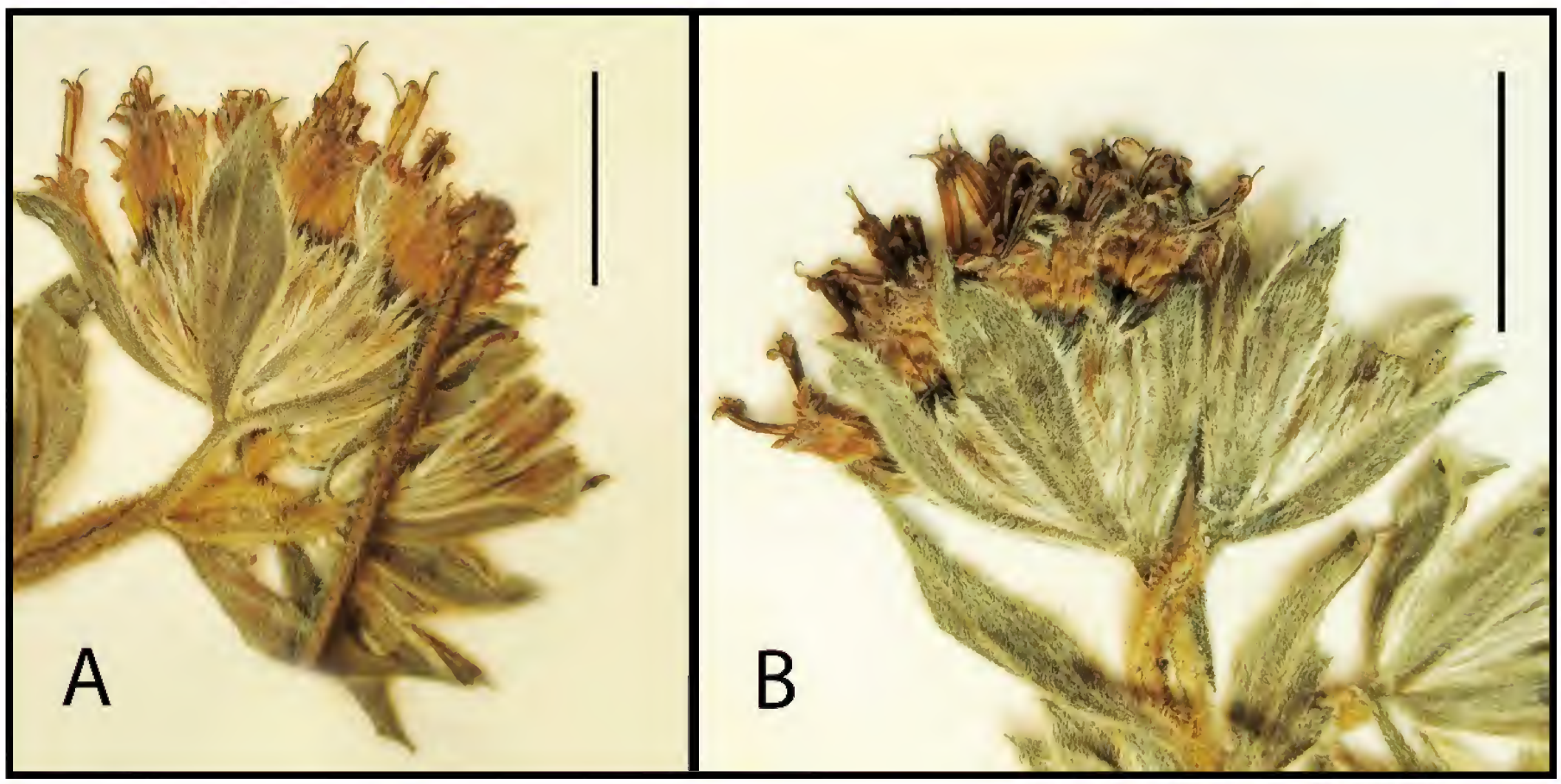

Figure 5. *Lagascea espinalii*, cymose glomerate-synflorescences showing leafy bracts of the false involucres partly obscuring the true involucres of the individual component capitula. (From the holotype, *Zapata 2147*, JAUM). Scale bars 1 cm.

Paratypes. COLOMBIA. Antioquia. Mpio. Peque, sector La Muñeca, cerca de la quebrada "peque", margen izquierda del Río Cauca, 515 m, 16 Apr 2014, *D. Zapata & J. Calle 495* (JAUM-64433); Mpio. Santa Fe de Antioquia, sector La Chorquina, vía a Urabá 10 km antes de Cativo, Bs-T, transición, vegetación secundaria, 1253 m, 5 Nov 2018, *D. Zapata 2148* (JAUM-2 sheets); Mpio. Santa Fe de Antioquia, sector La Sapera, vía a Urabá, Bs-T, talud, borde de carretera, 853 m, 24 Dec 2018, *D. Zapata 2151* (JAUM, as "2151 (1/2)").

Eponymy. *Lagascea espinalii* commemorates the late Luis Sigifredo Espinal Tascón, for whom the Herbario Luis Sigifredo Espinal-Tascón of the Universidad del Valle in Cali is named. Espinal is well-known for his 1960s collections with Jose Cuatrecasas in Valle de Cauca, and species from there named for him include *Brunellia espinalii* Cuatr., *Hypericum espinalii* N. Robson, and *Pleurothallis espinalii* Luer. Luis Sigifredo Espinal is the author of several fine treatments of vegetation types of Colombia (e.g., Espinal and Montenegro 1963; Espinal 1989, 1990), and in particular those of Antioquia (e.g., Espinal 1964, 1985). He was for many years a professor at Universidad Nacional de Colombia sede de Medellín and *Magnolia espinalii* (Lozano) Govaerts named in his honor is based on his material from Antioquia. It is altogether fitting and proper to dedicate this Compositae—*Lagascea espinalii*—from Antioquia to Luis Sigifredo Espinal Tascón.

Distribution and ecology. *Lagascea espinalii* is endemic to Antioquia in northwestern Colombia, where it is known from municipios Peque and Santa Fe de Antioquia. The species is found from about 500–1250 meters elevation and flowers from November–December(+ April). The synflorescences are often beetle-damaged affecting seed set, as has been noted (Schilling and Panero 2011) in other Helianthinae. *Lagascea espinalii* grows in open areas of seasonally dry forested canyons and in transitional zones with bordering "bosque humedo premantano" (viz map in Espinal 1985: 63) of the Cauca River basin between the Cordillera Central and the older volcanic Cordillera Occidental. Espinal (1985) and Vélez (2004) gave the upper elevational range of Cauca basin dry forests as 1000 meters, but material at 1253 meters elevation is from a dry area, which was designated by Diego Zapata (in sched.) as "Bs-T, transición" (bosque seco tropical, transition).

Colombian dry forests (bosque seco tropical) have been referenced as “bs-T” by Espinal and Montenegro (1963) and Espinal (1989, 1990), who stated their average annual rainfall is between 1000–2000 mm. Gentry (1995) said "categorization” of low rainfall sites as dry forest is "straightforward" noting there is a close correlation between rainfall regimes and “recognizable dry forest.” Studies of Colombian pollen deposits reveal Pleistocene Epoch floristic shifts, with dry glacial maxima lowering sea levels and causing downslope "displacement of vegetation" belts (Simpson Vuilleumier 1971; van der Hammen 1974). Sarmiento (1975) and Gentry (1982) noted the current formations of dry forests in Colombia were influenced by “increasing dry climatic regimes of the Pliocene and Pleistocene” epochs. Sarmiento (1975) and Gentry (1995) mapped the dry forests of Colombia, and showed them to be isolated from each other forming "a chain of dry islands." Gentry (1982) and Vélez (2004) noted the high endemism in Colombian dry forests.

Dry forests in Antioquia were mapped by Espinal (1985: 25), and include those along the Cauca River, as well as an isolated zone about 40 kms further west, between Uramita and Dabeiba. Vélez (2004) provided an excellent floristic survey of the seasonally dry forested canyons of the Cauca River basin in Antioquia. Pizano and García (2014: 11) also mapped dry forests (in bright green) along the Cauca River in Antioquia, but not those between Uramita and Dabeiba. Espinal (1989) provided a profile between Medellín and Turbo (on the east side of the Golfo de Urabá), and schematically diagramed the dry canyon along the Cauca River near Santa Fe de Antioquia, basically where *Lagascea espinalii* appears to be endemic. The low-end bordering "bosque humedo premantano–bh-P" that Espinal (1985: 62) gave as at about "900" meters elevation are equivalent to the transitional zone indicated by Diego Zapata (in sched.), and presumably have at least some shared characters and influences with seasonally dry tropical forests.

The most detailed maps that I have seen of seasonally dry forests in Colombia are those of IGAC (1983: planchas 5-05 and 5-08), where this zone is labeled as “Wa.” These fairly detailed maps show Colombian dry forests as discontinuous along the length of the Cauca River, and plotted in detail the Cauca River basin tropical dry forests in Antioquia. In Antioquia, the dry forests in the Cauca River basin are mapped at their southern limit near Pintada. Pintada is about 90 kms south of Santa Fe de Antioquia at about 5° 50' N latitude, near the border with Caldas. The Cauca River basin dry forests in Antioquia reach their northern limit near Puerto Valdivia about 75 kms northeast of Santa Fe de Antioquia at about 7° 10' N latitude. The few localities of *Lagascea espinalii* known to me are within a few kms of the south-north flowing Cauca River, three near Santa Fe de Antioquia, and original collection about 50 kms north of the colonial city (i.e., from about 6° 34' N latitude to 7° 00' N latitude). The range of *Lagascea espinalii* thus falls completely within the 150+ km-long zone (ca. 180 km by river, fide Álvaro Idárraga, pers. comm.) of Cauca River basin dry canyons in Antioquia. It seems possible that further collections of *Lagascea espinalii* may de discovered in similar dry canyons between the known localities or elsewhere within the 150+ km-long Cauca River seasonally dry forests in Antioquia or adjacent Caldas. Similarly, the Mexican-Central American lagasceas (except for *L. mollis* and *L. helianthifolia*; viz maps in Stuessy 1978 and Turner 2015) are mostly restricted to the relatively dry Pacific watershed.

Figure 6. *Lagascea helianthifolia*, showing leaves subsessile and subauriculate and several terminal, sessile, glomerate synflorescences appearing as a single capitulum; the corollas are white and not as yellowish as seen in this figure. (From Robert Sweet, British Flower Garden, vol. 3, tab. 215. 1827–1829, as *Nocca latifolia*).

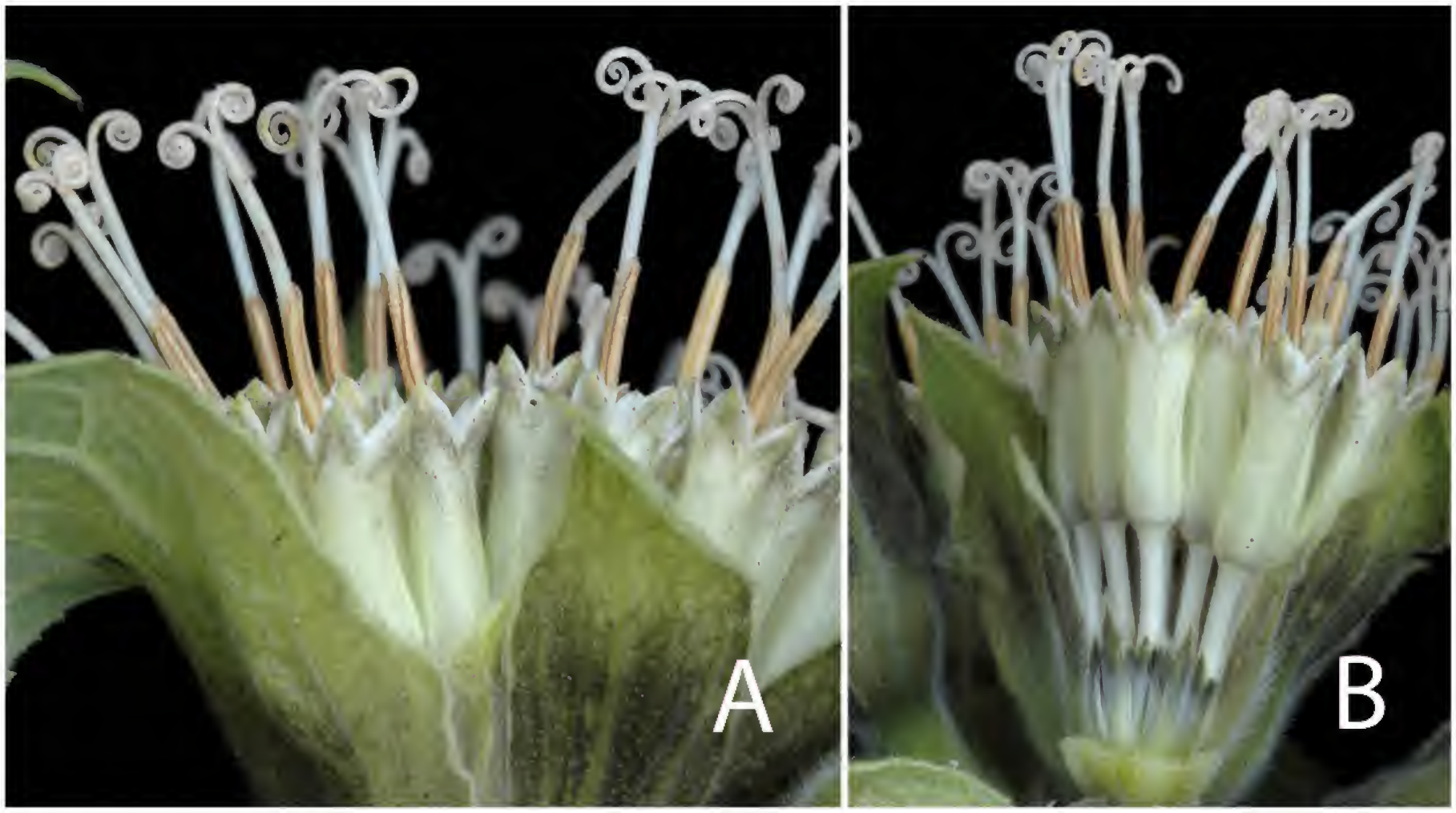

Figure 7. Synflorescences of *Lagascea helianthifolia*. A. Synflorescence showing leafy bracts of the false secondary involucre and exserted florets. B. Synflorescence with a large leafy bract removed, revealing several uniflorous capitula with short gamophyllous true involucres. The styles of this species are typically well-exserted. *Pedro Tenorio Lezama s.n.*, same species as *Pedro Tenorio Lezama 21374*, Oaxaca, Mexico; photographs by the collector.

About 20 Compositae species were reported as endemic to Antioquia by Pruski and Funston (2011), of which only five (*Perymenium colombianum* B.L. Turner, and two species of each of *Clibadium* and *Espeletia*) are Helianthoids. The *Perymenium* is obviously radiate-capitulate, and the Espeletias are páramo caulirosulates. The clibadiums, although moderately low-elevational and shrubby, are opposite-leaved, heterogamous, and disciform-capitulate (marginal florets pistillate and disk florets functionally staminate). None of these five previous mentioned Antioquian endemic Helianthoid species are likely to be confused with *Lagascea espinalii*. *Acanthospermum hispidum* DC., *Lagascea mollis* Cav., *Melanthera nivea* (L.) Small, *Pectis elongata* Kunth, *Pectis linearis* La Llave, and *Tridax procumbens* L. are other widespread Neotropical Heliantheae sensu lato found in Antioquia only in the Cauca River basin (Pruski & Funston 2011): none are endemic to Antioquia. *Lagascea espinalii* is thoroughly distinctive, without sympatric close relatives, and is the only Composite endemic to the Cauca River basin in Antioquia, Colombia.

The isolated, seasonally dry, inter-Andean valleys of the Cauca River drainage where *Lagascea espinalii* occurs, are found intermittently along the river system's length, have a flora very distinct from adjacent wetter mountains, and a high percentage of regional endemism (Gentry 1982; Vélez 2004). *Lagascea espinalii* fits well morphologically within the Mexican-centered, strange genus *Lagascea* (Compositae: Heliantheae: Helianthinae), and its endemism to Cauca River seasonally dry forests in Antioquia is noteworthy. The detection of narrowly endemic *L. espinalii* is testament to the regional endemism and under-collected aspect of inter-Andean seasonally dry forests, and shows that novelties awaiting discovery may remain, even in the most well-trodden genera.

Figure 8. Uniflorous capitula of *Lagascea helianthifolia.* A. Two capitula showing sericeous involucres with unequal lobes, and elongate corolla tubes. B. Dissected capitulum, showing adaxial glabrous surface of involucre (lower right) with unequal teeth and the main nerve of each phyllary with an elongate resinous glands, an immature ovary (lower left), and a corolla tube and throat. C. Dissected floret with corolla limb opened and showing adaxial surface, lobes with intramarginal nerves, anthers (upper left), and sericeous involucre (bottom). (From *Croat & Hannon 64179*, MO, from Honduras). Metric scales lower left.

Key to species of *Lagascea*

1. Diffusely branched herbs; involucres with vertical lines of several small round glands; (minutely coroniform-fruited); (*Lagascea* sect. *Lagascea*).

2. Corollas yellow; anthers yellow to light brown; peduncles strigose; (west-central Mexico) ..... **Lagascea aurea** Stuessy
2. Corollas white; anthers dark brown to black; peduncles stipitate-glandular; (Pantropics) ..... **Lagascea mollis** Cav.

1. Shrubs; involucres with vertical lines of 1–few elongate glands.

3. Corollas golden-yellow; synflorescences globose, single; pappus often rudimentary; (*Lagascea* sect. *Calhounia*).

4. Individual capitula with involucre lobes linear-lanceolate, 1–4 mm long; secondary involucre bracts strigose and sometimes stipitate-glandular; (southern Oaxaca, Mexico to southern Arizona) ..... **Lagascea decipiens** Hemsl.
4. Individual capitula with involucre lobes triangular-lanceolate, 0.2–0.3 mm long; secondary involucre bracts subglabrous to short-setulose; (west-central Mexico) ..... **Lagascea palmeri** (B.L. Rob.) B.L. Rob.

3. Corollas white (-pinkish); synflorescences campanulate, grouped terminally; pappus biaristate; (*Lagascea* sect. *Nocca*).

5. Leaf blade apices acuminate to long-attenuate; disk corolla tubes relatively short, about 3–4 times shorter than corolla throat, about as long as the longest pappus arista; (narrowly endemic to Cauca river basin in Antioquia, northwestern Colombia) ..... **Lagascea espinalii** Pruski
5. Leaf blade apices acute-acuminate; disk corolla tubes relatively long, usually 1–2 times shorter than corolla throat, much longer than longest pappus arista.

6. Leaves mostly 10–20+ cm long, subsessile and/or reticulate-veined abaxially, often subauriculate basally; (northern to southern Mexico, Guatemala, Honduras, El Salvador, Nicaragua) ..... **Lagascea helianthifolia** Kunth
6. Leaves mostly 3–9(–13) cm long, petiolate and surfaces smooth to weakly reticulate abaxially, obtuse to attenuate basally.

7. Leaf blades strongly discolorous, abaxial surfaces sericeous; (west-central Mexico) ..... **Lagascea heteropappa** Hemsl.
7. Leaf blades more or less concolorous, abaxial surfaces strigillose to strigose(-tomentose).

8. Leaf blades lanceolate to oblanceolate, apices broad-acute–obtuse, adaxial surfaces strigose, not nitidous; (western Mexico) ..... **Lagascea angustifolia** DC.
8. Leaf blades elliptic-ovate, apices usually acute, adaxial surfaces nitidous (west-central Mexico) ..... **Lagascea rigida** (Cav.) Stuessy

Noteworthy range extensions

FLORESTINA LATIFOLIA (DC.) Rydb. [**Bahieae**]. First South American voucher of the genus *Florestina*. **COLOMBIA. Santander.** Mpio. Los Santos, Vereda El Pozo, sector N de La Mesa de Los Santos, calizas orientadas al Chicamocha, vegetación xerofitica, 1300–1500 m, 23 Sep 2004, *J.F. Fernández-Alonso et al. 22675* (COL-592763, HUA-169398). Figure 9.

The genus *Florestina* Cass. (formerly treated with typically paleate Heliantheae), contains six(-eight) species, and until now was thought to be distributed only from the southwestern United States into Mesoamerica, where three species occur (Turner 1963; Soto-Trejo et al. 2016; Pruski & Robinson 2018). One of these three Mesoamerican species, *F. latifolia*, was known previously to extend from Mexico southeastward into Nicaragua (Turner 1963; Dillon et al. 2001; Soto-Trejo et al. 2016; Pruski & Robinson 2018). Its disjunction from Nicaragua to South America is an uncommon pattern, albeit similar to that seen in *Oxylobus glandulifer* (Sch. Bip. ex Hemsl.) A. Gray ex Klatt, *Stenocephalum jucundum* (Gleason) H. Rob., and *Stevia incognita* Grashoff (Pruski & Robinson 2018). The reverse-directional pattern of taxa common in South America, and thence disjunct northwestward to Nicaragua, such as is reported in *Lessingianthus rubricaulis* (Bonpl.) H. Rob. and *Vernonanthura brasiliana* (L.) H. Rob. (Pruski & Robinson 2018), appears to be even less frequent.

Colombian species of epaleate tribe Bahieae include the widespread (southwestern United States to Chile) low-herbaceous, narrowly pinnatifid-leaved *Schkuhria pinnata* (Lam.) Kuntze ex Thell., but this species has been reported only at 2000+ meters elevation from central to southern Colombia, and is unknown in Antioquia. *Florestina latifolia* and *Schkuhria pinnata*, although each members of tribe Bahieae, are unlikely to be confused. Among regional Bahieae genera, *Florestina* is diagnosed by its herbaceous habit, leaves opposite proximally becoming alternate distally, discoid epaleate capitula, narrow-attenuate style branches, and symmetrically arranged pappus scales.

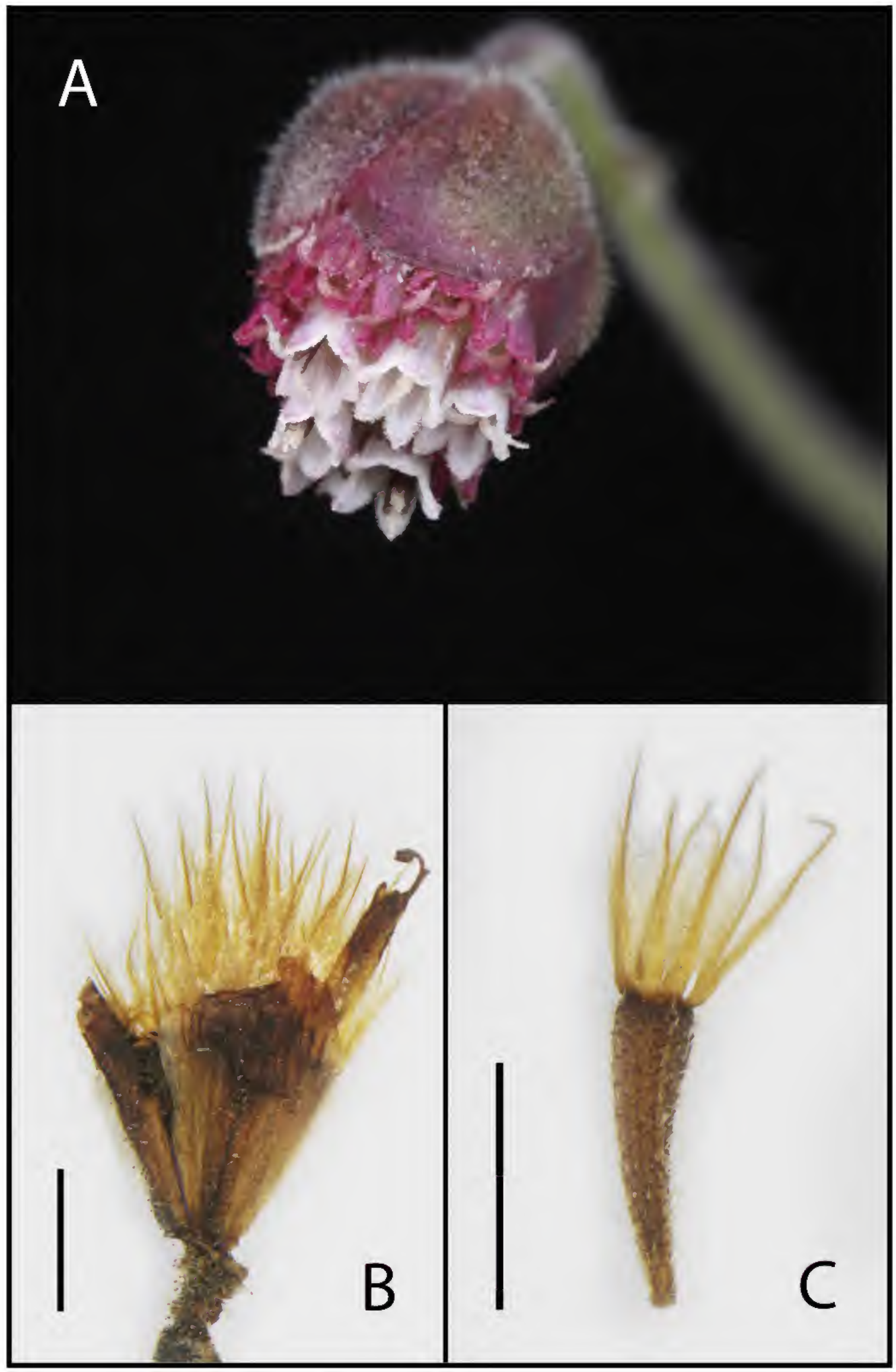

Figure 9. *Florestina latifolia*. A. Discoid epaleate capitulum, showing broad subequal phyllaries and corollas; marginal florets post-anthesis with corollas pinkish-red, central florets at anthesis with corollas cream-colored. B. Fruiting capitulum showing narrow-tipped pappus scales that are about as long as the fragmentary corolla (towards upper right). C. Cypsela with narrow-tipped pappus scales nearly as long as cypsela body. (A *Stevens & Montiel 28751*, from Nicaragua, photograph by Olga Martha Montiel; B–C *Fernández-Alonso et al. 22675*, COL). Scale bars 2 mm.

Florestina latifolia is distinguished by its simple leaves, capitula with broad subequal sparsely stipitate-glandular phyllaries, apically narrowed pappus scales nearly as long as the corollas but shorter than the cypselae, and corollas at anthesis that are cream-colored but post-anthesis turn pinkish-red (Fig. 9). The South American plants match the Mexican-Central American ones in critical morphological features, albeit on average having slightly longer pappus aristae. *Florestina platyphylla* (B.L. Rob. & Greenm.) B.L. Rob. & Greenm. is similar in gestalt, but differs by shorter pappus squamellae that are broadly rounded to truncate apically. *Florestina latifolia* typically occurs in rocky areas, dry forests, and savannas.

The determination here of Colombian *Fernández-Alonso et al. 22675* as *Florestina latifolia* extends the range of the species about 1700 kms to the southeast. This report represents the first known record of the genus *Florestina* in continental South America, and in turn a new record of the genus and species in Colombia. This range extension is not wholly unexpected, however, as the Colombian collection was labeled as occurring in "vegetación xerofitica," a common habitat of *Florestina latifolia*.

GONGYLOLEPIS COLOMBIANA (Cuatr.) Cuatr. [**Stifftieae**]. First Antioquian voucher of the genus *Gongylolepis*. **COLOMBIA. Antioquia.** [Cordillera Occidental], Mpio. Ituango, alto de Santo Domingo, 1800–2200 m, 21 Feb 1995, *F. Giraldo & M. Correa 413* (JAUM-24450).

Mutisieae s. lat. are a striking component of the Neotropical Flora, in that these species are often either trees, have large coriaceous leaves, or have large, colorful capitula. *Gongylolepis colombiana* was known previously only in Cordillera Oriental of Norte de Santander, Colombia, and Mérida and Táchira, Venezuela. Here, *Gongylolepis colombiana* is documented in Antioquia in the northern reaches of the Cordillera Occidental and vouchered by the newly determined, albeit collected two decades ago, *Giraldo & Correa 413* (JAUM). This collection thus represents a new record for both the Cordillera Occidental and for Antioquia, Colombia. The species should be expected in the Cordillera Central of Antioquia.

Gongylolepis R.H. Schomb. is a Guayana-centered genus with homogamous flowers with isomorphic, bilabiate corollas, and has been placed traditionally in tribe Mutisieae. *Gongylolepis* contains 14 species and is Guayana-centered, but one species, *Gongylolepis colombiana* (Cuatr.) Cuatr., is extra-Guayanan and is endemic to the northern Andes (Pruski 1989, 1991, 1997; Díaz-Piedrahita & Vélez-Nauer 1993). In its size and biogeography *Gongylolepis* is thus similar to *Stenopadus* S.F. Blake. *Stenopadus* contains 15 species, is also Guayana-centered but contains a single species, *Stenopadus andicola* Pruski, endemic to the Andes of Ecuador and Peru (Pruski 1991, 1997, 1998, 2010; Pruski & Beltrán 2003). Like *Gongylolepis*, *Stenopadus* is arborescent, homogamous, has isomorphic corollas, and large capitula, but *Stenopadus* differs from *Gongylolepis* by being discoid-capitulate. Moreover, at a glance the genera may be distinguished vegetatively: *Gongylolepis* has leaves stoutly clasping-based, whereas *Stenopadus* has leaves either narrowly petiolate or subsessile but non-clasping. This vegetative character was used to determine the collection in Antioquia: the JAUM sheet has only a single post-fruit capitulum but characteristic broad-based, clasping leaves.

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THE SPONTANEOUS OCCURENCE OF KIWIFRUIT, *ACTINIDIA CHINENSIS* VAR. *DELICIOSA* (ACTINIDIACEAE), IN OHIO

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ABSTRACT

Kiwifruit, *Actinidia chinensis* var. *deliciosa*, has been discovered from a wild site in Ohio, the first report of this species outside of cultivation in the state. It was collected in Hamilton County, in the southwest corner of the state, along a creek bank ca. 10 km north of the Ohio River.

Plants of *Actinidia chinensis* var. *deliciosa* (kiwifruit) have been reported to occur sporadically outside of cultivation in the eastern USA (see below). An apparently spontaneous occurrence of the species in Ohio is documented here.

Voucher specimen. Ohio. Hamilton Co.: Cincinnati, Spring Grove Cemetery and Arboretum, along the bank of Indian Creek in an undeveloped 300-acre area, 39.18331, -84.53964, ca. 185 m, 27 Aug 2017, *Conover s.n.* (CINC, MU).

A sewer outlet runs along Indian Creek at the Ohio site, and it is suspected that the seed may have arrived via the sewer. The species was reported in Kansas from along a sewer outlet (Serviss et al. 2012). During February 2018, the Ohio River and tributaries experienced the highest water levels since 1997, and most of the vegetation along the banks of Indian Creek, including the *Actinidia*, did not survive. It is thus not known whether or not the plant would have survived the winter. Nevertheless, the viny habit and the aggressive growth of this species raises concern that it could become a problematic invasive. When revisited two weeks after its initial discovery, the Hamilton County plant had increased considerably in size.

A survey of Ohio herbaria did not reveal any other collections of this species, nor have escapees from cultivation been observed (R. Gardner, ODNR, pers. comm.). The first report of a spontaneous occurrence outside of cultivation in the USA was published by Serviss et al. (2012) from a collection made in Arkansas. Herbarium specimens in online databases suggest the possibility of additional escapes from cultivation in Georgia (*Moore & Cruse 2256*, GA), Missouri (*Rimer s.n.*, MO), North Carolina (*Giencke s.n.*, NCU), Tennessee (*Estes & Beck 6861*, APSC; *Levy et al. 16305*, ETSU; *McCoy s.n.*, TENN), and Virginia (*Fleming et al. 15448*, NCU; *Fleming 16325*, GMUF).

In the USA, *Actinidia chinensis* var. *deliciosa* is hardy in zones 7a to 9b (NC Extension, n.d.). *Fleming et al. 15448* from Albemarle Co., Virginia (hardiness zone 7a/7b), was fruiting at the time of collection. The label of the *Rimer s.n.* collection from Howell Co., Missouri (hardiness zone 6b), states "plants invasive along bank of pond ..., very aggressive, never becoming fertile, dying back partially each winter but recovering the following spring." Hamilton Co., Ohio, which lies in the extreme southwest corner of the state, includes areas of zones 6a and 6b.

Figure 1. *Actinidia chinensis* var. *deliciosa.* Voucher for Ohio record reported here (*Conover s.n.*, CINC).

Figure 2. *Actinidia chinensis* var. *deliciosa* growing in uncultivated land in Cincinnati, Ohio. Top: Plant on 5 November 2017. Bottom: Stem with characteristic reddish brown, persistent pubescence.

Actinidia chinensis var. *deliciosa* is an herbaceous twining vine — it is perennial and becomes woody with age. It is native to the mountains of the Chinese interior between 800–1400 m (Huang & Ferguson 2001; Li et al. 2007). Seeds were first exported to France in 1899 and England in 1900. It is not known what became of the plants in France, but they appear not to have persisted. The plants grown in England generated interest among the gardening public, but they are believed to have all been functionally male and did not persist (Ferguson 1983; Testolin et al. 1995). The seeds that first arrived in the USA in 1904 may have been from the same collection as those first grown in England — similarly, they were all functionally male and did not produce fruit (Ferguson 2004).

The first successful introduction of kiwifruit outside of China took place in 1904, when Isabel Frasier carried seeds home to New Zealand following a visit to Yichang, China (Ferguson 2004). These seeds produced both male and female plants, and are the origin of today's kiwifruit industry, including the 'Hayward' cultivar which is the most widely cultivated and, until relatively recently, the only variety of 'kiwi' encountered by most consumers (Ferguson 1999). Kiwifruit is cultivated commercially in California and, on a much smaller scale, in other states.

The nomenclature of the cultivated kiwifruit has a relatively short but unsettled history – being first described less than 80 years ago – a history that is rife with disagreement and uncertainty. Auguste Chevalier first described the kiwifruit as *Actinidia latifolia* var. *deliciosa* A. Chev. from a plant cultivated at the Jardin des Plantes in Paris (Li et al. 2010). Shortly after publication, Chevalier realized that he had assigned his new taxon to the wrong species and in 1941 transferred it to *A. chinensis* as var. *deliciosa* (A. Chev.) A. Chev. Liang and Ferguson (1984) raised the taxon to specific rank, as *A. deliciosa* (A. Chev.) C.F Liang & A.R. Ferguson. Since then, considerable debate has centered around whether the taxon merits specific or varietal rank (see Li et al. 2000), and both are frequently seen in the literature. This present report follows the taxonomy of Li et al. (2007).

Actinidia chinensis var. *deliciosa* (A. Chev.) A. Chev. has gone by a number of common names including kiwifruit, kiwi, bowerberry, tara vine, Chinese gooseberry, and the Chinese *mei wei mi hou tao*.

Three other species of *Actinidia* are cultivated in Ohio: *A. arguta* (Siebold & Zucc.) Planch. ex Miq., *A. kolomikta* (Maxim. & Rupr.) Maxim., and *A. polygama* (Siebold & Zucc.) Maxim. Actinidia arguta, which is hardy in zones 3–8, has been documented out of cultivation in Cuyahoga County in northeast Ohio (Wilder & McCombs 2002) and appears to be becoming problematically invasive in the northeastern USA (BEAT et al, 2019). Actinidia kolomikta has been cultivated at The Dawes Arboretum in Newark, Ohio (D. Johnson, pers. comm.), but it has not been documented out of cultivation in Ohio. Cultivation of A. polygama (silver vine) in Ohio has not been recorded in recent years, but the species was praised as an attractive climber in 1897 by the Ohio State Horticultural Society (Carr 1898). Actinidia chinensis var. deliciosa can be easily distinguished from the other three species by the pubescence on the stems, which is more or less densely strigose with reddish brown trichomes. Stems of the other three species are glabrous to occasionally glabrate (*A. arguta*) with whitish trichomes. Similarly, the fruits of *A. chinensis* var. *deliciosa* are densely pubescent, whereas those of the other species are glabrous.

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NOMENCLATURAL NOVELTIES FOR THE VASCULAR FLORA OF NEW MEXICO

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ABSTRACT

The following nomenclatural novelties are proposed: **Acmispon plebeius** (Brandeg.) Allred, **comb. et stat. nov.**; **Chenopodium neomexicanum** Standley var. **arizonicum** (Standl.) Allred, **comb. et stat. nov.**; **Gilia lyndana** Allred, **nom. et stat. nov.**; **Houstonia nigricans** (Lam.) Fernald var. **papillacea** (B.L. Turner) Allred, **comb. nov.**; **Leptoloma pubiflorum** (Vasey) Wippf & Shaw var. **syrticola** (Wippf & Shaw) Allred, **comb. et stat. nov.**; **Monarda citriodora** Cerv. ex Lag. var. **pectinata** (Nutt.) Allred, **comb. et stat. nov.**; **Oenothera capillifolia** Scheele var. **gayleana** (B.L. Turner & M.J. Moore) Allred, **comb. et stat. nov.**; **Oenothera hartwegii** Benth. var. **pubescens** (A. Gray) Allred, **comb. in stat. nov.**

In preparation for an upcoming revision of the *Flora Neomexicana* series (Allred 2012a, 2012b; Allred & Ivey 2012), the following nomenclatural novelties are proposed for names of vascular plants found in New Mexico.

AMARANTHACEAE/CHENOPODIACEAE

Chenopodium neomexicanum Standl. var. **arizonicum** (Standl.) Allred, **comb. et stat. nov.** Basionym: *Chenopodium arizonicum* Standl., N. Amer. Fl. 21(1): 19. 1916. **TYPE: USA. Arizona.** Pima Co.: Fenced area, Santa Rita Forest Reserve, "September 27 to October 4," 1903, *D. Griffiths 5982* (US 497569, image!).

GRAMINEAE

Leptoloma pubiflorum (Vasey) Wippf & Shaw var. **syrticola** (Wippf & Shaw) Allred, **comb. et stat. nov.** Basionym: *Leptoloma syrticola* Wippf & Shaw, Phytoneuron 2018-46: 4. 2018. **TYPE: USA. Texas.** Winkler Co.: 9.5 mi S on Hwy 18 from its intersection with Hwy 115 in Kermit then 16.9 mi on County Rd 404 from its intersection with Hwy 18, along roadside near fence line in Jalmar loamy fine sand, 16 Jun 1987, *J.K. Wipff 308* (TEX, image!).

LABIATAE

Monarda citriodora Cerv. ex Lag. var. **pectinata** (Nutt.) Allred, **comb. et stat. nov.** Basionym: *Monarda pectinata* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 25. 1848. **TYPE: USA. New Mexico.** Santa Fe Co.: Near Santa Fé, *W. Gambel s.n.* (not located, not at PH).

LEGUMINOSAE

Acmispon plebeius (Brandeg.) Allred, **comb. nov.** Basionym: *Hosackia plebeia* Brandeg., Proc. Calif. Acad. Sci., ser. 2, 2(11): 144. 1889. *Lotus oroboides* (Kunth) Ottley var. *plebeius* (Brandeg.) Ottley, Brittonia 5: 107. 1944. *Lotus plebeius* (Brandeg.) Barney, Great Basin Naturalist 46: 257. 1986. **TYPE: MEXICO. Baja California.** El Rancho Viejo, 30 Apr 1889, *T.S. Brandegee s.n.* (UC 80720, image!).

ONAGRACEAE

Oenothera capillifolia Scheele var. **gayleana** (B.L. Turner & M.J. Moore) Allred, **comb. et stat. nov.** Basionym: *Oenothera gayleana* B.L. Turner & M.J. Moore, Phytologia 96: 200, figs. 1–4. 2014. **TYPE: USA. Texas.** Culberson Co.: 13.1 mi E along FM 652 from its intersection with US 62/180, bare gypsum hills, 25 May 2004, *B.L. Turner 24–255* (TEX, image!).

Oenothera hartwegii Bentham var. **pubescens** (A. Gray) Allred, **comb. in stat. nov.** Basionym: *Oenothera greggii* A. Gray var. *pubescens* A. Gray, Smithsonian Contr. Knowl. 3: 72. 1852. *Calylophus hartwegii* (Benth.) Raven subsp. *pubescens* (A. Gray) Towner & Raven, Madroño 20: 243. 1970. *Oenothera hartwegii* Benth. subsp. *pubescens* (A. Gray) W.L. Wagner & Hoch, Syst. Bot. Monogr. 83: 212. 2007. **TYPE: USA.** Expedition from Western Texas to El Paso, New Mexico, May–October, 1849, *C. Wright 199* (GH 00263632, image!).

POLEMONIACEAE

Gilia lyndana Allred, **nom. et stat. nov.** Replaced synonym: *Gilia ophthalmoides* Brand subsp. *australis* A.D. Grant & V.E. Grant, Aliso 3: 263, map 11, fig. 15D. 1956. *Gilia flavocincta* A. Nels. subsp. *australis* (A.D. Grant & V.E. Grant) A.G. Day and V.E. Grant, Aliso 5: 484. 1964. Non *Gilia australis* (H. Mason & A.D. Grant) V.E. Grant & A.D. Grant, Aliso 3: 87. 1954. Non *Gilia splendens* Douglas ex H. Mason & A.D. Grant subsp. *australis* H. Mason & A.D. Grant, Madroño 9: 213. 1948. **TYPE: USA. Arizona.** Pima Co.: Santa Catalina Mountains, Sabino Canyon, 26 Mar 1905, *J.J. Thornber s.n.* (ARIZ 27239, image!). Note: The epithet honors Lynda Sue Street Allred (b. 1949), beloved companion and wife of nearly 50 years of Kelly W. Allred.

RUBIACEAE

Houstonia nigricans (Lam.) Fernald var. **papillacea** (B.L. Turner) Allred, **comb. nov.** Basionym: *Hedyotis nigricans* (Lam.) Fosberg var. *papillacea* B.L. Turner, Phytologia 79: 15, 20, fig. 1–3. 1995. **TYPE**: **USA. New Mexico.** Otero Co.: Northern McKittrick Canyon at first crossing of Texas-New Mexico boundary on the New Mexico side, gravels and boulders of stream bottom, riparian type habitat and below protected cliffs, big tooth maple, ponderosa pine, madrone, etc., 8 Oct 1973, *T.F. Patterson 508* (LL, image!).

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ERAGROSTIS SUPERBA (POACEAE) NEW TO THE FLORA OF LOUISIANA

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ABSTRACT

Eragrostis superba is reported as new to Louisiana. It occurs abundantly in a power line right-of-way within Walter B. Jacobs Memorial Nature Park northeast of Shreveport.

During a recent survey of plant diversity in Walter B. Jacobs Memorial Nature Park, I found what appeared to be an unusual grass growing abundantly along a power line right-of-way. I identified it as *Eragrostis superba* Peyr. and sent specimens to Chris Reid and Charles Allen, who confirmed the identification as a species previously unreported for the Louisiana flora.

Voucher. Louisiana. Caddo Par.: Walter B. Jacobs Memorial Nature Park, 3 mi W of Blanchard, just northeast of Shreveport, power line right-of-way, soils of the acidic Guyton series, ca. 500 culms in an area of 1.5 acres, 21 Oct 2019, *Kelley 157* (LSUS).

The plants were found only along the disturbed roadbed on the north side of the right-of-way opening. This area is dominated by native herbaceous plants such as *Andropogon*, *Liatris*, *Tridens*, and *Rudbeckia* species. The roadbed has been traveled frequently and graded after updates to the power line in 2018 — the open area is managed by mowing. The area was reseeded from a Texas native seed mix, which may have contained *Eragrostis superba* seeds, or the seeds may have been brought in by tire treads.

Eragrostis superba is a perennial, warm-season bunch-grass. It is native to Africa and naturalized in North America after being introduced to rangelands for use in revegetation and drought tolerance (Diggs et al. 2006). Rapid growth, high seed production, and high seedling vigor give the species the potential for aggressive colonization (USDA, NRCS 2014).

Eragrostis superba is known to occur in at least 31 counties in Texas, New Mexico, Arizona, and Oklahoma (Kartesz 2014; USDA, NRCS 2014). The range as reported by BONAP is significantly smaller than that of the iNaturalist citizen-science app for the state of Texas. iNaturalist also shows a sharp increase in sightings since 2016. Collection data suggest that the species escaped cultivation in this region as early as 1954 (SERNEC Data Portal 2019).

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Chris Reid (LSU, School of Renewable Natural Resources) and Charles Allen (Allen Acres) confirmed the identification and reviewed the manuscript. Daniel Mills provided information about the power line maintenance and will monitor the species on-site.

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NEW TO OKLAHOMA: *TRIADICA SEBIFERA* (EUPHORBIACEAE)

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ABSTRACT

This paper documents occurrences of the exotic *Triadica sebifera* (Chinese tallow) in southeastern Oklahoma. Previous reports of this species in the state referred to a single, planted specimen. These new records indicate that the tree is naturalizing in McCurtain County.

An occurrence of *Triadica sebifera* (L.) Small from Marshall Co., Oklahoma is cited in BONAP (2019) and EDDMaps (2019). The Center for Agriculture and Bioscience International, however, specifically lists this tree as a cultivated, planted specimen (2019) — it is actually located on the grounds of the Marshall County Courthouse (Mike Proctor, pers. comm.). Naturalized occurrences do exist in southeastern Oklahoma in McCurtain County (Figure 1). Thirteen individuals were present at Unit 20 of the Red Slough Wildlife Management Area (RSWMA), a USDA Forest Service Wetland Reserve project south of the town of Haworth. At least three of the thirteen were mature and producing fruits, and root sprouting was also noted (Figures 2 and 3). These trees, as well as any visible seeds have since been destroyed. An additional fruiting tree was found at unit 27b of RSWMA, approximately 1.0 km south of those in Unit 20. Associated species at both sites included *Ampelopsis arborea*, *Apios americana*, *Campsis radicans*, and *Baccharis halimifolia*. A single tree was found in the city of Idabel (also McCurtain County), growing out of the side of a small, possibly man-made, pond that had been recently cleared of all other vegetation, including *Pontederia cordata* and *Alternanthera philoxeroides*. Its location in relation to the pond indicates that it was not planted.

Vouchers. **Oklahoma.** McCurtain Co.: Red Slough Wildlife Management Area, Unit 27b, N33.74295° W94.65758°, 29 Aug 2019, *Buthod, Hoagland, & Arbour AB-12313* (OKL); Idabel, pond area behind Museum of the Red River, 33.879398 -94.819994, 30 Aug 2019, *Buthod & Hoagland AB-12275* (OKL).

Triadica sebifera is a tree in the Euphorbiaceae native to southern China, Taiwan, and Vietnam. In East Asia, the species is economically important for timber and dye manufacturing and for the waxes and oils found in its seeds (Wurdack 2016). *Triadica sebifera* was first introduced into the USA in the 1700s. Today, it is found in Alabama, Arkansas, California, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Texas (EDDMaps 2019; Kartesz 2015; USDA, NRCS 2019). It is assumed to be extirpated from Kentucky, where a single individual was found and destroyed (Comley 2008; Wurdack 2016).

Figure 1. Locations of *Triadica sebifera* in Oklahoma.

Benjamin Franklin is frequently cited (or blamed) for its early appearance in the USA; he sent seeds to the Georgia colony in 1772, noting the tallow to be "a most useful Plant" (National Archives 2019). Most of the naturalized trees in the USA are instead, however, descended from seeds introduced in the early 1900s by the USDA for use as an oil crop and for soap-making (DeWalt et al. 2011; Miller 2003; USDA, NRCS 2019). In the USA today it is mainly utilized as an ornamental landscape plant. It also is a major nectar source for domesticated honeybees (Lieux 1975).

Figure 2. Fruiting specimen of *Triadica sebifera*, Red Slough Wildlife Management Area, McCurtain Co., Oklahoma.

Figure 3. Root sprouting of *Triadica sebifera*, Red Slough Wildlife Management Area, McCurtain Co., Oklahoma.

Triadica sebifera can grow in a variety of soil types and habitats. It readily spreads to wet areas, including the banks of rivers and streams, ditches, and coastal wetlands, and it is tolerant of high salinity, drought, shading, and flooding (Miller 2003; Texas Invasive Species Institute 2014). It can also grow in drier upland sites and has the ability to invade undisturbed forests, replacing entire stands of native trees (EDDMapS 2019; Wurdack 2016). The species is considered noxious in Florida, Louisiana, Mississippi, and Texas (USDA, NRCS 2019). The species produces great quantities of pollen, and its flower architecture allows it to be pollinated by several generalist species of bees (Clark & Howard 2019). Chinese tallow can form root sprouts, and its seeds are dispersed by birds and water (USDA, NRCS 2019).

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A NOVEL SPRING-FLOWERING *LIRIOPE* (ASPARAGACEAE) FROM CENTRAL CHINA

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ABSTRACT

Liriope vernalis Avent & Floden, **sp. nov.**, is described and illustrated from specimens originating from northeastern Sichuan Province, China. This species of *Liriope* is the earliest of the genus to come into the flower. Molecular phylogenetic analyses of the nuclear ribosomal ITS region support its distinction.

Liriope Lour. is a genus of 8–10 species that occurs across the Himalaya, China, Indochina, Japan, the Philippines, and Taiwan (Chen & Tamura 2000; Conran & Tamura 1998). Considerable taxonomic work has been devoted to *Liriope* and its sister genus *Ophiopogon* Ker Gawl (Bailey 1929; Wang & Tang 1951; Hume 1961; Hsu & Li 1981; Fantz 1993, 1994, 2008a, 2008b, 2009; Nesom 2010; Lattier et al. 2014), largely within the realm of horticulture due to their prolific use as a border and groundcover. Despite the attention to the systematics of *Liriope* and study of genome size and polyploidy (Lattier et al. 2014), there is no consensus on the number of species within *Liriope*.

Nesom (2010) provided an account of *Liriope* and *Ophiopogon* species in cultivation, recognizing *L. muscari* (Dcne.) L.H. Bailey and noting the distinctiveness of *L. platyphylla* F.T. Wang & Tang, while acknowledging that further study might reveal additional justifiable species in the *L. muscari* complex. Wang et al. (2014) included multiple samples of *L. platyphylla* in their phylogenetic analyses of *Ophiopogon* and these formed two sister clades, indicating molecular differentiation among the samples. Recently Xia et al. (2012) described *L. zhejiangensis* Xia & Li, which they presumed to be placed in the *L. muscari* group. Since the late 1990's, a distinctive *Liriope* originating from Sichuan Prov., China, has been cultivated in the USA and sold as "*L. vernalis*," an invalid name. Here we validate that name with a diagnosis, description, and designation of a type specimen, and we provide preliminary molecular data that support its distinction from other species.

Methods

DNA from *Liriope vernalis* (from the type collection) was extracted using D'Neasy Plant Minikits (Qiagen, Foster City, California), following manufacturer's protocols. PCR protocols followed Schilling et al. (2007) but used primers ITS4 and ITS-Leu. Sequencing was done at the University of Tennessee Genomics Core.

Other sequences of *Liriope*, *Ophiopogon*, *Peliosanthes*, and *Tupistra* were included from Genbank. Phylogenetic analyses and sequence comparisons were performed in Geneious 7.1.7 (Biomatters Ltd.). Alignments were done in MAFTT v7.017 (Katoh et al. 2002) and RaxML 7.2.8 (Stamatakis 2006) was used to assess relationships, with 1000 iterations to provide bootstrap support values.

Results

The results of the molecular analyses of ITS show *Liriope vernalis* embedded in an unresolved clade containing multiple disparately placed samples of *L. platyphylla* and *L. muscari* (Genbank number MH558170). The phylogeny recovers a paraphyletic *L. muscari* with respect to *L. spicata* in one clade and *L. vernalis* and *L. platyphylla* in the other clade (Fig. 1). *Liriope graminifolia* is sister to a clade with *L. muscari* and *L. spicata* samples, and this clade is in turn sister to the remainder of the unresolved samples, which includes *L. platyphylla*, *L. muscari*, and *L. vernalis*. Notably, *L. kansuensis* is included with *Ophiopogon*. The placement of *L. spicata* var. *prolifera* within the two samples of *L. muscari* is also noteworthy.

Sequence comparisons of the sample of *Liriope vernalis* show between 98–99% pairwise similarities (between 5–9 bp) relative to other *Liriope* in the *L. muscari* complex and down to between 94–97% pairwise similarity to the two *L. graminifolia* samples. Some changes are shared with *L. graminifolia* and others with some samples of *L. muscari*, with one fixed difference from all other *Liriope* samples available in Genbank.

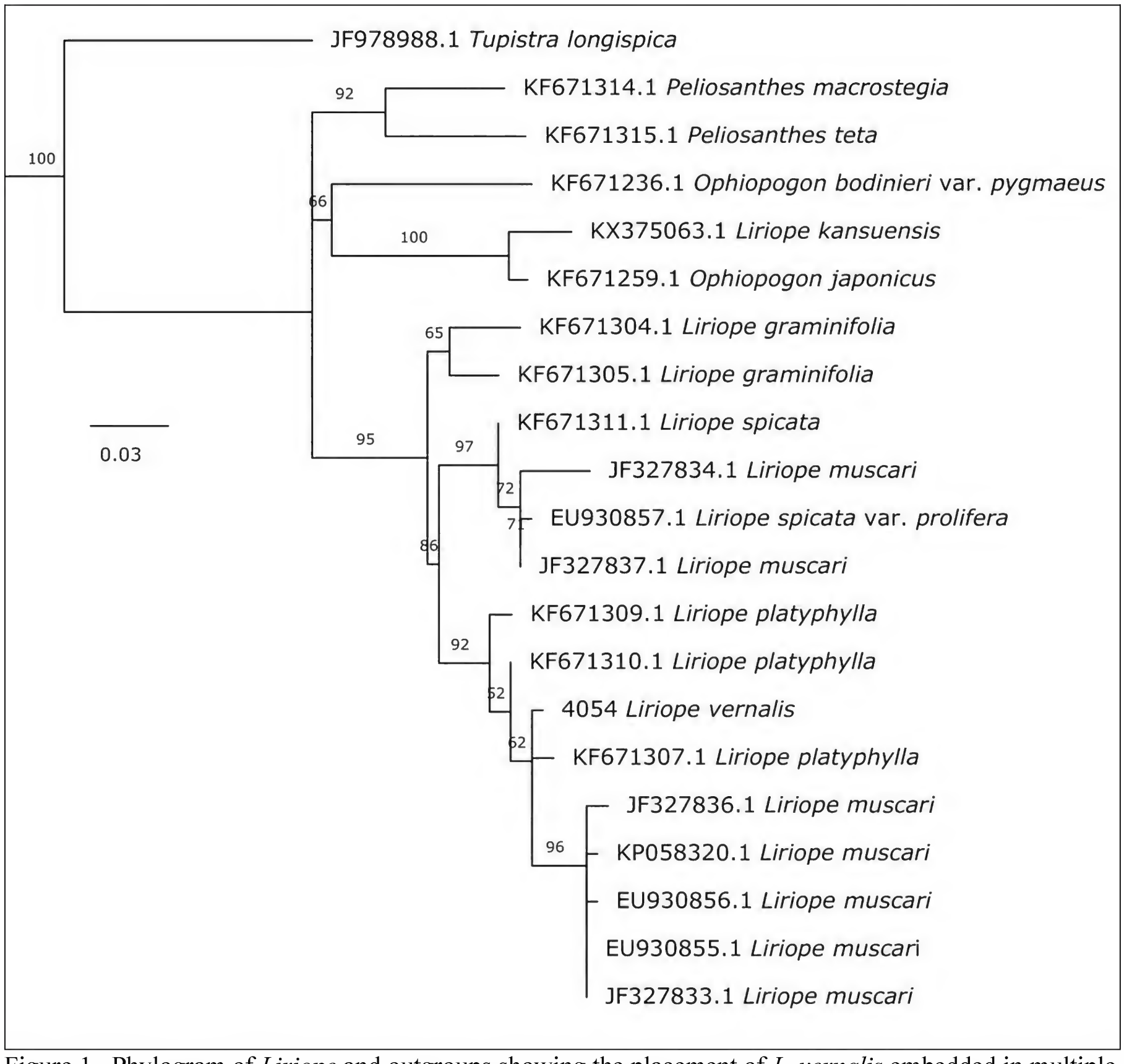

Figure 1. Phylogram of *Liriope* and outgroups showing the placement of *L. vernalis* embedded in multiple samples of *L. muscari* and *L. platyphylla*; derived from 500 maximum likelihood replications in RaxML.

Results of the molecular analyses of *Liriope* (Fig. 1) suggest that the evolutionary structure of *Liriope* is more complex and diverse than currently recognized. *Liriope vernalis* differs in ITS sequence from all other samples in Genbank. Both *Liriope muscari* and *L. platyphylla* likely comprise more than one entity, based on their polyphyly in the phylogeny and observable differences in morphology of accessions in cultivation. These results also support the treatment of Nesom (2010) in treating *L. muscari* and *L. platyphylla* as different species and shows that additional investigation is required to understand their taxonomy. Most accessions of *L. muscari* form the ultimate clade, but two others are placed with *L. spicata*. *Liriope platyphylla* samples form an unresolved grade with *L. vernalis* between them. The lack of resolution of *L. platyphylla* might be due to polyploidy that has led to genetic divergence between accessions (it has diploid and tetraploid forms—see Lattier et al. 2014) or simply due to limited sampling. Placement of *Liriope kansuensis* with *Ophiopogon* may be due to misidentification of the sample. Additionally, some of the samples of *L. muscari* in the *L. spicata* clade may be due to misidentifications. Future phylogenetic work should document the ploidy of accessions to determine monophyly of different ploidy levels of the same taxon and should be based on consistently identified vouchers.

LIRIOPE VERNALIS Avent & Floden, **sp. nov.** **TYPE**: **CHINA**. Sichuan Province. [N of Wanyuan], N 32°09.425', E 108°02.351', 2940 ft elevation, gentle slopes to almost flat area in heavy, red clay below open 30' tall pine forest (type of red pine), only *Mahonia* and tall *Liriope* here, *D. Probst CPC 5.5.01.1*, pressed from specimens cultivated by Avent and Floden from the original wild collection, collected on 7 May 2017 by AJF (holotype: MO; isotypes: CAS, NY, P, PE, US). Figures 2–4.

Differs from *Liriope longipedicellata* F.T. Wang & Tang (Fl. Reipubl. Pop. Sin. 15: 257. 1978) its roots with fusiform tubers (vs. without tubers), leaves 7–9-veined and not glaucous abaxially (vs. 5-veined and glaucous), the flower pedicels only 2–3 mm (vs. 5–8 mm), and with larger tepals 6–7 mm (vs. ca. 3 mm), and from *L. muscari* by the terminal pedicel articulation (vs. articulation at mid pedicel), leaves with fewer veins (7–9 vs 9–11), longer staminal filaments, and anthers shorter than the filaments. Differing from all *Liriope* species in its early spring flowering period (beginning late April to early June vs. July to September).

Perennial, essentially caespitose herbs, slowly increasing in clonal size through production of short rhizomes. Rhizomes 0.5–1 × 1–2 cm long, fleshy white-yellow. Roots thick, with fusiform tubers, tubers 0.5–2 cm long. Cataphylls (scale leaves) 2–14 cm long, purple-brown when fresh, apex callose, margins 2–4 mm wide, papery and membranous, center 9–12-veined. Leaves linear, 20–55 × 0.3–0.6 cm, apex obtuse, coriaceous, 7–9 veined, margins antrorsely scabrellous, ca. 10 teeth/mm. Scapes erect, dark green, 30–60 cm long including inflorescence, ridged in transverse section; inflorescence 10–20 cm with 15–30 nodes with flowers (naked for 2/3 of scape). Flowers in clusters of 3–7, typically 2–4; bracts near basal part of inflorescence up to 1 cm long, ovate-caudate acuminate, bracts near middle broadly ovate-lanceolate, and at distal portion linear lanceolate and only 2–3 mm long, bracteoles ca. 1 mm long; pedicel purple, 2–3 mm long, articulate at apex; tepals free, 6–7 × 0.2–0.3 mm, ovate-elliptic; anthers yellow, 1.7–2 mm, filaments 2–2.5 mm long; ovary ca. 1.5 mm, globose, shoulders slightly squared, style ca. 2 mm, stigma capitate; seeds black at maturity, globose, 5–8 mm in diameter. Flowering April–June, fruiting August–September.

Other specimens examined. CHINA. **Gansu Province**. Wen Xian, Motianling Shan, Baishui Jiang Nature Reserve, vicinity of town of Fanba, upstream along Heiyin Gou, remnant mixed deciduous forest with *Acer*, *Ulmus*, *Juglans*, *Castanea*, *Diospyros*, *Cercis*, etc., most remaining trees of economic importance, 32°42'12"N, 105°5'48"E, 825-890 m, dry slopes in forest and around ledges, 13 May 2007, *Boufford & Zhang 37608* (GH). **Hubei Province**: W Hupeh, May 2000, *Wilson 489*, as "*L. spic*. v. *longipes* var. *nov. Wang & Tang"* (K 846088, digital image). **Shaanxi Province**: Zhenping Co., Zhongbao Town, Jinping Village, 1800 m, 20 Jun 2005, *Chen et al 2829* (WUK 0495024 digital image <http://www.cvh.ac.cn/spm/WUK/0495024>).

Figure 2. A selected clone of *Liriope vernalis* in a propagation bed flowering at Juniper Level Botanic Garden from the seed collection from which the type gathering was made from. Photograph by Tony Avent, May 2017. This clone began from a seed collection in 2001.

Figure 3. Line drawing from the holotype of *Liriope vernalis, D. Probst CPC 5.5.01.1* (MO). A. Whole culm. B. Single branch of the inflorescence scape. C. Anther and ovary. D. Basal scale leaves. E. Bracts of the inflorescence. F. Close up of leaf margin showing veins and scabrellous margin. Scale bars, A= 2 cm, B = 2 mm, C = 2 mm, D = 5 cm, E = 0.5 cm, F = 2 mm.

Figure 4. *Liriope vernalis* cultivated by AJF — a 7-year-old plant begun from a single seed-grown shoot from the same seed lot that the type originated from. This plant was removed from a 3-gallon pot and cleaned of growing medium. Clonal size increases slowly through short rhizomes — stolons are not produced. Root tubers are abundant. Top left: Whole clump. Top right: Root tubers. Bottom left: New shoot and center portion of plant dying out after 7 years of growth. Bottom right: Rhizome broken off from clump.

Figure 5. *Liriope vernalis* cultivated by AJF. New growth points adjacent to previous seasons shoots. From the same clump illustrated in Figure 4.

Liriope vernalis is known only from the Daba Shan in southeastern Gansu, southern Shaanxi, northeastern Sichuan, and western Hubei provinces, China. The distribution of this species is sympatric with that of the narrow endemic *L. longipedicellata* and also with *L. muscari*, though neither was observed near the type locality in May or September 2015 by AF. It occurs in grassy areas and open woodland at elevations of 800–1700 meters. Given the minimal number of collections that are documented (though over an expansive region), it should be considered data deficient (DD, IUCN 2017).

Flowering in *Liriope vernalis* begins in late April to early May and continues into early June. The epithet *vernalis* alludes to the early spring-flowering, well before all other species begin inflorescence growth. Infructescences with immature fruit are often present when sympatric species begin to flower. *Liriope longipedicellata*, which is endemic to the same region of China, begins flowering in July and can continue into September. The flowering period of *Liriope* is typically summer (Chen & Tamura 2000). In contrast, *Liriope vernalis* flowers early in the season before sympatric species and they are often in early fruit (in cultivation) before other species of *Liriope* have begun to flower. The only other species reported to flower as early as May is *L. spicata* (Chen & Tamura 2000), from which *L. vernalis* is well-differentiated in morphology by its non-stoloniferous and densely caespitose habit, more than 5-veined leaves, and its larger perigone. The type of *L. zhejiangensis* was collected on May 7, but the range of flowering dates of this species in the description is given as July–August. It and *L. vernalis* are well morphologically separated from one another in numerous characters.

Morphological delimitation of *Liriope* species is aided by characters that include whether plants are caespitose vs. mat-forming by stolons and/or rhizomes, the presence of root tubers, the number of lines on the abaxial leaf surfaces, the point of articulation on the flower pedicel, and the length of the anthers vs the stamen filaments (Hsu & Li 1981; Chen & Tamura 2000). Hsu and Li (1981) documented the significance of the presence or absence of stolons and rhizomes in species delimitation; these characters were also used by Chen and Tamura (2000). *Liriope vernalis* is distinctly clump-forming with very short rhizome internodes (essentially caespitose) and no production of stolons or longer rhizomes over a decade of cultivation by both authors (Fig. 4). It also produces root tubers in contrast to the sympatric *L. longipedicellata* and has more abaxial leaf veins, shorter pedicels, and larger tepals. *Liriope muscari* and *L. platyphylla* that were recovered in the same clade (Fig. 1) differ in their longer pedicels and subequal anthers and filaments.

Key to caespitose species of *Liriope*
(adapted from Chen & Tamura 2000 and Nesom 2010)

1. Pedicels 2–3 or 5–8 mm long; anthers slightly shorter than filaments.
    2. Roots without fleshy tubers; leaves glaucous abaxially, 5-veined; pedicels 5–8 mm long; tepals ca. 3 mm long ..... **Liriope longipedicellata**
    2. Roots with fleshy tubers; leaves not glaucous abaxially, 7–9-veined; pedicels 2–3 mm long; tepals 6–7 mm long ..... **Liriope vernalis**
1. Pedicels (2–) 4–5 mm long; anthers subequal to filaments.
    3. Scapes 20–30 cm long, rachis 6–12 cm long; fascicles 35–50; perigone tube short, <0.5 mm; anthers 1.5 mm long; anthers 1.6–1.8 mm long; bracts with hyaline margins to near apex ..... **Liriope muscari**
    3. Scapes 55–60 (–100) cm long, rachis 18–24 cm long; fascicles 60–80; perigone tube 1–1.2 mm long; anthers 1.5 mm long; bracts with hyaline margins basally ..... **Liriope platyphylla**

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NEW COMBINATIONS IN *HELIOTROPIUM* FOR FOUR NEW WORLD SPECIES OF *TOURNEFORTIA* (HELIOTROPIACEAE, BORAGINALES)

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ABSTRACT

Four new combinations are provided in *Heliotropium* for New World species previously known as species of *Tournefortia*: **Heliotropium album** (Splitgerber ex De Vriese) Feuillet, **comb. nov.**, **Heliotropium cuspidatum** (Kunth) Feuillet, **comb. nov.**, **Heliotropium melanochaeta** (DC.) Feuillet, **comb. nov.**, and **Heliotropium ulei** (Vaupel) Feuillet, **comb. nov.**

Recently, with the support of morphological and molecular studies of the Boraginaceae sensu lato, Diane et al. (2002), Gottschling et al. (2001, 2004), and Hilger & Diane (2003) have provided good arguments for the resurrection of families corresponding to the subfamilies of the Boraginaceae sensu lato. In this classification (Luebert et al., 2016), the order Boraginales includes eleven families: Boraginaceae sensu stricto (ca. 90 genera / 1600–1700 species), Codonaceae (1 / 2), Coldeniaceae (1 / 1), Cordiaceae (2 / ca. 400), Ehretiaceae (7 / ca. 150), Heliotropiaceae (4 / ca. 450), Hoplestigmataceae (1 / 2), Hydrophyllaceae (12 / 240–260), Lennoaceae (2 / 4), Namaceae (4 / ca. 75), and Wellstediaceae (1 / 6). Most of those conclusions have been adopted by Stevens for the Angiosperm Phylogeny Webside version 14 (accessed 20 Nov 2019).

Resulting from the study of the Heliotropiaceae, the generic limits have been reconsidered. The genera *Euploca* Nutt. and *Myriopus* Small have been resurected to accomodate respectively in one hand, *Schleidenia* Endl., *Hilgeria* Förther, and *Heliotropium* L. sect. *Orthostachys* R. Br. subsect. *Axillaria* I.M. Johnst. and on the other hand, *Tournefortia* L. sect *Cyphocyema* I.M. Johnst. Furthermore, the remaining part of *Tournefortia* (sect. *Tournefortia*) has been merged in *Heliotropium*.

Only a few species of *Tournefortia* sect. *Tournefortia* have a name in *Heliotropium*. New combinations are formally made here to accomodate four *Tournefortia* species in *Heliotropium*.

1. Heliotropium album (Splitgerber ex De Vriese) Feuillet, **comb. nov.** Basionym: *Tournefortia alba* Splitgerber ex DeVriese, Nederl. Kruidkund. Arch. 1: 347. 1848. **TYPE**: **Surinam**. *Splitgerber 841* (holotype: L!; isotype: P!).

= *Tournefortia bicolor* Sw., Prodr., 40. 1788. *Tournefortia hirsutissima* f. *bicolor* (Sw.) D.L. Nash, Fl. Veracruz 18: 141. 1981. **TYPE**: **Jamaica**. *Swartz s.n.* (S [photo!]). Not *Heliotropium bicolor* Hochst. & Steud. = **Euploca strigosa** (Willd.) Diane & Hilger

Distribution—West Indies, Central and South America.

2. Heliotropium cuspidatum (Kunth) Feuillet, **comb. nov.** Basionym: *Tournefortia cuspidata* Kunth, in H.B.K., Nov. Gen. Sp. (quarto ed.) 3: 83. 1818. **TYPE**: **Ecuador**. Guayas, near Guayaquil, *Humboldt & Bonpland s.n.* (holotype: P! [photo F-039107]; isotype: P!).

= *Tournefortia obscura* A. DC., Prodr. 9: 517. 1845. **TYPE**: **Guyana**. Kwitaro River, *R.H. Schomburgk 1st series 571* (holotype: G–DC [microfiche!]; isotypes: BM, G, K-2! [scans!], L!).

Distribution—West Indies, Central and South America.

3. Heliotropium melanochaeta (DC.) Feuillet, **comb. nov.** Basionym: *Tournefortia melanochaeta* DC., Prodr. 9: 520. 1845. **LECTOTYPE** (designated by Johnston 1935: 56): **French Guiana**. 1821, *Martin s.n.* (holotype: G-DC!; isotypes: GH, P!).

Distribution—Guyana and French Guiana. To be expected in Surinam.

The species name is a substantive in apposition; therefore, the gender should not be changed. The Greek "chaeta" means bristle.

4. Heliotropium ulei (Vaupel) Feuillet, **comb. nov.** Basionym: *Tournefortia ulei* Vaupel, Notizbl. Bot. Gart. Berlin–Dahlem 6: 186. 1914. **LECTOTYPE** (here designated): **Bolivia**. Rio Madeira, Porvenir, Jan 1912, fl & fr, *Ule 9711* (K!).

= *Tournefortia miquelii* J.F. Macbr., Proc. Amer. Acad. Arts 51: 541. 1916. **TYPE**: **Surinam**. Surinam River near Bergendal, *Focke 1308* (holotype: L!).

Distribution—Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, and the Guianas.

The presumed holotype of *Tournefortia ulei* Vaupel was kept at the Königl. botanischen Gartens und Museums in Berlin-Dalhem. It was destroyed during WW II and is only known by a photograph at the Field Museum in Chicago (F-1063!). I here designate the only duplicate I know of *Ule 9711*, kept at the Royal Botanic Garden, Kew, as the lectotype.

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TAXONOMIC SUMMARY OF *HETEROTHECA* (ASTERACEAE: ASTEREAE): PART 1, SECTS. *HETEROTHECA* AND *AMMODIA*

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ABSTRACT

Part 1 of an overview of the North American genus *Heterotheca* is presented. Included are 8 species of sect. *Heterotheca* and 3 species of sect. *Ammodia*. Species of sect. *Phyllotheca* (the *H. sessiliflora* group) and sect. **Heterotheca** sect. **Chrysanthe** Nesom, **sect. nov.**, will be treated in forthcoming publications. **Heterotheca mayoensis** Nesom, **sp. nov.**, is recognized along with four new nomenclatural combinations: in sect. *Heterotheca* — **Heterotheca rosei** (Wagenk.) Nesom, **comb. et stat. nov.** and **Heterotheca viridis** (Nesom) Nesom, **comb. et stat. nov.**; in sect. *Ammodia* — **Heterotheca rudis** (Greene) Nesom, **comb. nov.**, and **Heterotheca scaberrima** (A. Gray) Nesom, **comb. et stat. nov.** Details of typification, a detailed distribution map, and at least a diagnostic description are provided for each species. A lectotype is designated for *Heterotheca* sect. *Gymnactis* DC. and an epitype is designated for *H. psammophila* Wagenk.

The North American genus *Heterotheca* has been divided in previous taxonomy into three main groups: (1) sect. *Heterotheca*, annuals and perennials that produce epappose ray achenes; (2) sect. *Ammodia*, perennials without ray flowers; and (3) sect. *Phyllotheca* sensu lato, which has included the largest number of taxa in the genus, all perennial with pappose ray achenes. In the present study, the concept of sect. *Phyllotheca* is limited to the 10 species of the *H. sessiliflora* group and the remaining species are conglomerated as sect. *Chrysanthe*.

Heterotheca sect. **CHRYSANTHE** Nesom, **sect. nov.** **TYPE**: *Heterotheca villosa* (Pursh) Shinners

Perennials; capitular bracts present or absent; ray florets present; disc corolla lobes glabrous or sparsely hairy with relatively short trichomes; ray and disc achenes both with inner and outer pappus.

Sect. *Chrysanthe* includes all species remaining after sects. *Ammodia*, *Heterotheca*, and *Phyllotheca* have been segregated. It perhaps represents a plesiomorphic and non-monophyletic matrix of species from which specialized groups have arisen. Harms (1963, his Ph.D. dissertation) proposed a name at sectional rank for this heterogeneous group, typified by *Heterotheca villosa*, but the name was never effectively published.

Most of the taxa of sect. *Heterotheca* are Mexican endemics; the ranges of *H. grandiflora* and *H. subaxillaris*, and *H. psammophila* are primarily in the USA. Sect. *Ammodia* is limited to the Pacific Coast region (California, Oregon, and Washington). Sect. *Phyllotheca* is mostly restricted to coastal and near-coastal regions along the Pacific from Baja California north into central California, with one outlyer in northwestern Sonora and one in the California Sierra. Most of sect. *Chrysanthe* occurs in the central and western USA and Canada but one small group has radiated in Mexico and one species is primarily in the eastern USA.

The preliminary cladistic analysis of *Heterotheca* in Brouillet et al. (2009, p. 598; redrawn here as Fig. 1), which shows 12 species, suggests that while sects. *Ammodia*, *Heterotheca*, and *Phyllotheca* (as treated here) may be monophyletic, sect. *Chrysanthe* probably is not. Instead, it perhaps is a plesiomorphic matrix from which specialized groups have arisen.

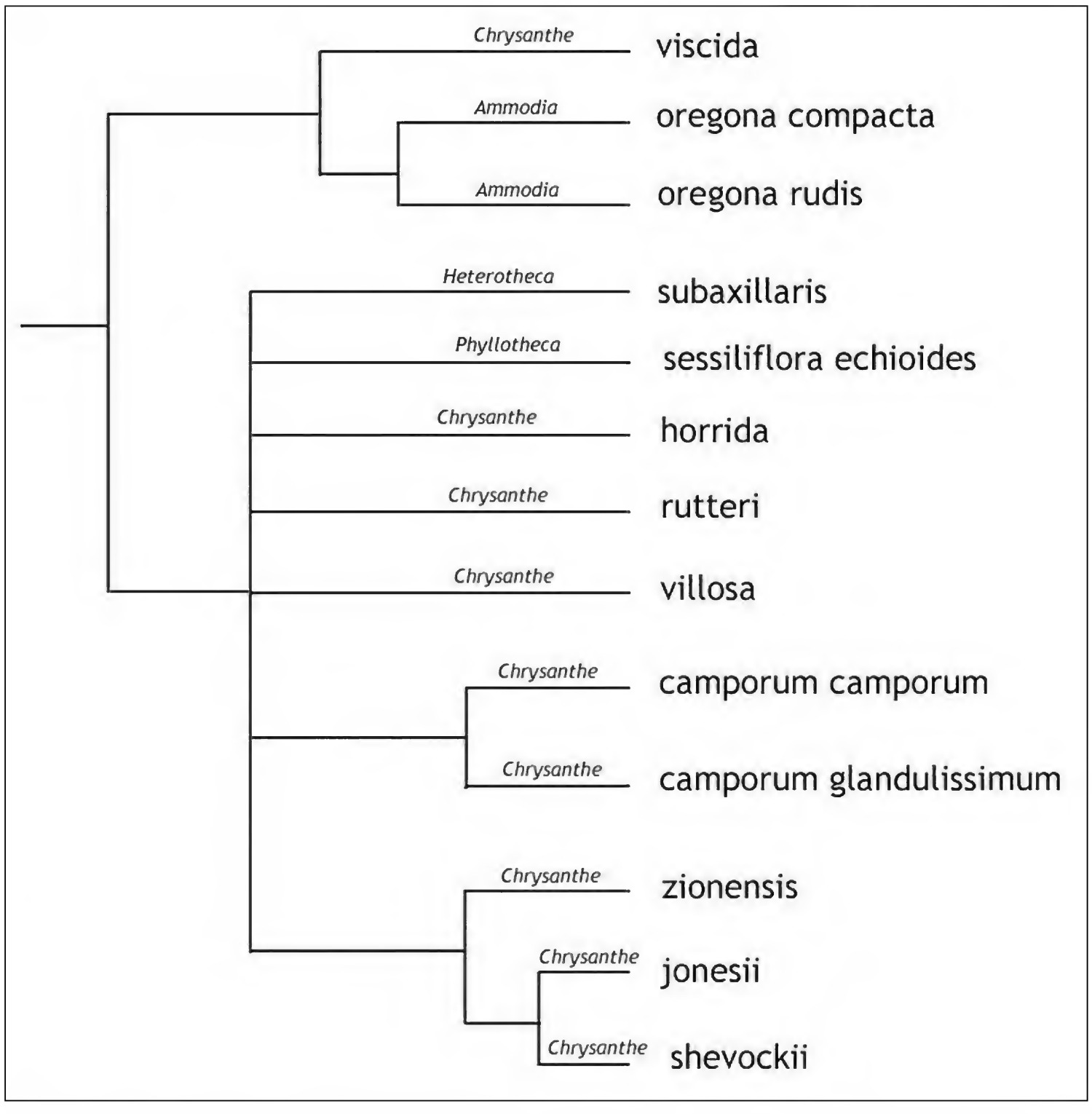

Figure 1. Cladistic relationship of 12 taxa of *Heterotheca* as determined from a parsimony anlysis of ITS sequence data in Brouillet et al. (2009); extracted and redrawn from their Figure 37.1E. The taxon shown here as "subaxillaris" was labeled as "fulcrata subaxillaris" in the diagram by Brouillet et al., but the pertinent molecular data were taken from Morgan (1997), who identified that species as *Heterotheca subaxillaris*. Section names reflect the present taxonomy.

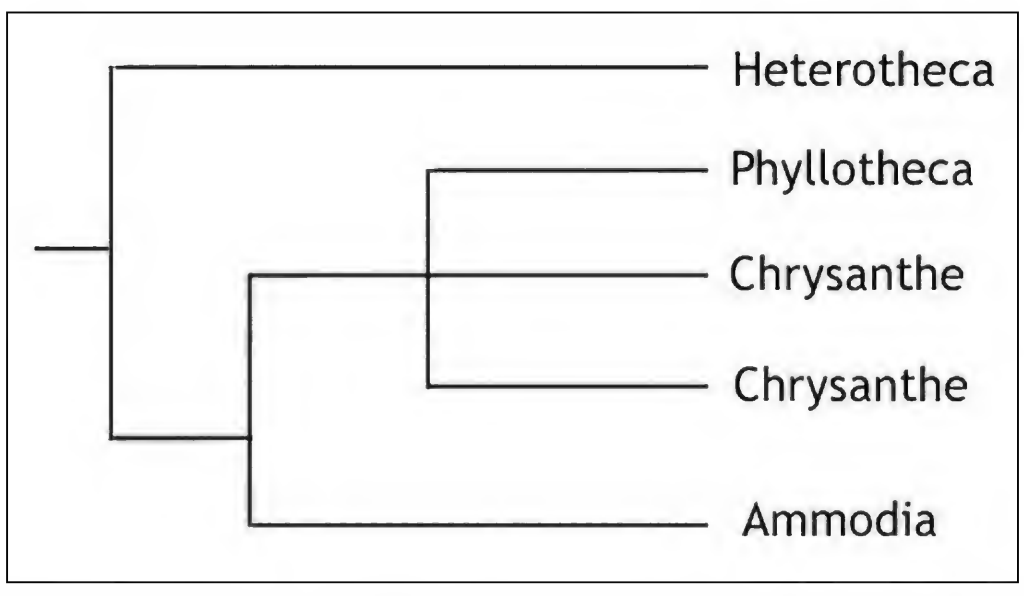

Figure 2. Relationships among sections of *Heterotheca* as intuitively hypothesized by Semple (1996, Fig. 3), using names as in the current study. Semple's "*sessiliflora* group" is identified here as sect. *Phyllotheca*, the larger part of his sect. *Phyllotheca* here as sect. *Chrysanthe*.

Taxonomic studies of *Heterotheca* have been published over the last 60 years (see Literature Cited and references in the text where pertinent), especially by Semple for sects. *Ammodia* and *Phyllotheca*, for sect. *Heterotheca* by Wagenknecht, Harms, and Nesom, and for sect. *Phyllotheca* by Shinners, Harms, Nesom, and others. Chromosome counts have been published mostly by Harms and by Semple and colleagues (see Literature Cited). Semple included chromosome numbers as part of the description for most of the taxa in his 1996 revision; many of those counts have been documented in publication (Semple 2008). A large set of his chromosome vouchers is deposited at MO (as well as other herbaria) and has been examined during the present study.

Diploids and tetraploids occur within many species of *Heterotheca*; some species may be consistently diploid and a few apparently are consistently tetraploid. Many of the polyploids appear to be closely similar in morphology to diploids of the same species. No single widespread species has yet been studied in enough detail to characterize its overall ploidal constitution with high confidence.

The most comprehensive of prior taxonomic studies has been that of Semple (1996), which recognized 20 species and 20 additional (non-typical) varieties as comprising the genus. Semple commonly has used trinomials and quadrinomials to express the taxonomic structure — in his view, *Heterotheca sessiliflora* includes 6 entities at varietal rank divided among 4 subspecies; *H. oregona* includes 4 varieties; *H. fulcrata* includes 4 varieties; *H. villosa* includes 10 varieties. He allowed that infraspecific taxa of a single species may be sympatric, sometimes even in 4 geographically overlying "layers" (e.g., within *H. sessiliflora*, within *H. fulcrata*, within *H. villosa*).

For concepts of subspecific and varietal ranks, Semple referred (1996, p. 108) to his earlier study of the genus *Xanthisma* (Semple 1974). In his view, subspecies are discontinuously distinct in morphology, except for a few hybrids, and have allopatric distributions. Varieties are populations distinct within the species but characteristically sympatric with populations of different varieties and with populations of morphological intermediates. Variation is continuous among the varieties, although "the continuum would have pronounced modes."

For many of the taxa of sect. *Phyllotheca*, Semple's maps and specimen citations show collections identified as "aff. [taxon] (close to or approaching [taxon]." For the most part, the implications of Semple's notation seem to be that the taxa are widely variable (plastic) and that hybridization and introgression have blurred earlier-established evolutionary boundaries (the present treatment also recognizes and cites variants and putative hybrids). For example, "Within species, intervarietal hybrids are common in areas of sympatry" (Semple 1996, p. 24). In *Heterotheca villosa* "Each variety mostly likely evolved in isolation and adapted to a different set of habitat parameters" but "The highly plastic nature of the species and undoubted hybridization [after secondary development of sympatry of the varieties] make identification to variety difficult in numerous cases" (p. 108). In *H. fulcrata* (with 4 sympatric varieties) "Many intermediate forms occur throughout the range, and pure and mixed populations occur in areas of sympatry" (p. 70).

Semple's interpretations also are constrained by his use of numerical analyses in developing concepts of taxa. "Multivariate morphological analyses were undertaken on more than 600 specimens including 76 type specimens" (1996, p. 2), but those studies are unpublished.

Taxonomic perspectives of the current study

Distinct morpho-geographic entities can be discerned in *Heterotheca* and such entities are treated here mostly at specific rank. The degree of morphological distinction varies among species, and the genus includes widely distributed and narrowly distributed species. Despite a generally perceived difficulty in *Heterotheca* taxonomy, the morpho-geographic patterning recognized here does not seem extraordinary, because such is the case in most other genera, even in those thought to comprise many recently evolved species and probably with low overall genetic divergence among the species.

Perhaps the most significant problem in *Heterotheca* taxonomy has been that morphological and geographical boundaries of putative evolutionary entities simply have not previously been clearly discerned — this is reflected here in the revivification of various old names, description of previously unrecognized species, and modified definitions of previously accepted species. Other problems in the taxonomy of *Heterotheca* are related to several factors.

(1) Morphological differences among species involve relatively few classes of features.

Beyond features diagnostic at sectional rank, significant morphological features distinguishing *Heterotheca* taxa first are density and orientation of vestiture (especially on stems, including glands), presence/absence of capitular bracts, and arrangement of heads. Plant habit, degree of ciliation of leaf and bract margins, and head size also may be distinctive. As interpreted here, production of capitular bracts (foliaceous bracts immediately or closely subtending the involucre) is generally consistent within a species — but populational variation sometimes exists. Orientation of cauline vestiture also appears to be generally consistent within a species — hairs usually either are upwardly oriented (antrorsely, loosely to closely appressed) or spreading (irregularly so, stiffly patent, or sometimes deflexed at a slight angle); exceptions to this occur. Hairs sometimes appear to be distinctly "2-storied" — with a relatively dense understory and sparser, longer overstory, although this, too, sometimes is variable within a species.

(2) Infraspecific variation in morphology and ecology is considerable.

Knowledge of geographic boundaries closely underlies the validity of this observation, as recognition of the total geographic range of a species allows an understanding of its morphological and ecological variability. I have been aware of the potential for circular reasoning. Marked variability also may point to the possible existence of unrecognized entities or to the effects of hybridization. Or, in some species, especially those geographically isolated, it simply may point to an underlying matrix of genetic latitude.

(3) Parallel/convergent trends of variation among species are common.

This is a corollary of the relatively few classes of features that allow recognition of morpho-geographic entities and the numerous entities that can be recognized.

(4) Hybridization and introgression appear to be significant processes.

Recognition of putative hybrids (morphological variants outside the limits constrained by the genome of a particular species) is possible with knowledge of the distribution of species and their areas of sympatry. For example, in Colorado, the characteristically high-elevation *Heterotheca pumila* is a variable species apparently within the limits of its genome; further variation at lower elevations apparently often results from hybridization with other species. Where *H.* "*hispida*" and *H. villosa* are sympatric, intermediates and intergrades apparently are extensive, although the consistent occurrence in both of plants of typical morphology implies that some degree of reproductive isolation is in effect. The same relationship apparently holds between the Great Plains species *H. villosa* and *H.* "*ballardii*." Other species exist in sympatry without apparent gene flow.

In sum, the taxonomy of *Heterotheca* has been perceived as difficult, and so it is, but evolution has produced relatively discrete morpho-geographic entities and their recognition is not an intractable problem. Widely distributed taxa exchanging genes with others in areas of sympatry are maintained here at specific rank (in contrast to recognizing conspecific sympatric entities). And to some extent, the account of the genus presented here reflects how underlying philosophy of approach and taxonomic tenets can affect perceptions of evolutionary patterning.

Identification of goldenasters using this treatment

Because of infraspecific variation, parallelism and convergence, and the apparent frequency of hybridization, I have not attempted to provide a key that includes all of the taxa. It would have been a personally frustrating task and use of such a key at best probably would have been discouraging for others as well. Accuracy and expertise in identifications are possible, however, especially if correctly identified collections are available for reference. With the distribution maps and the diagnostic descriptions provided for each taxon, the present treatment should be of practical

use in identifying plants at hand. Once the morphology and geography of the species is understood, keys for smaller regions, where species occur in smaller numbers and with more apparent distinction among themselves, will be easier to construct.

Remaining problems

Further study, especially at local and regional levels, will surely result in modifications of the taxonomy presented here. Interesting problems can be found in any corner of *Heterotheca* taxonomy or geography, and at least some of these are pointed out. Several species treated here as widespread and variable will be interesting for further study and it seems likely that it will be useful to recognize additional narrowly distributed endemics at specific rank. Detailed study of chromosome numbers may be a relatively simple way to discover evolutionary patterns.

ACKNOWLEDGEMENTS

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HETEROTHECA Cass., Bull. Sci. Soc. Philom., s. 3, 1817: 137. 1817. *Hysterionica* sect. *Heterotheca* (Cass.) Baill., Hist. Pl. 8: 155. 1886. **TYPE**: *Heterotheca lamarckii* Cass., nom. illeg. (*Inula subaxillaris* Lam., *Heterotheca subaxillaris* (Lam.) Britt. & Rusby)

HETEROTHECA SECT. HETEROTHECA

Calycium Ell., Sketch Bot. South Carolina 2: 339. 1824 [1823], nom. illeg. **TYPE**: *Chrysopsis scabra* (Pursh) Ell. (= *Heterotheca axillaris* (Lam.) Britt. & Rusby).

Elliott included the description of *Calycium* after the entry for "9. SCABRA." of the genus *Chrysopsis* and intended *Calycium* as a potential alternate genus name for *Chrysopsis scabra*, noting this in prelude: "The two preceding species differ in habit from this genus and the C. Scabra very much, in the structure of the seed and pappus. If the double or exterior pappus should be found to form permanent generic distinctions, and to unite those species which in habit, symmetry and character agree, this plant must be separated from this genus. It may be distinguished by the following character."

Diplocoma Don in Sweet, Brit. Fl. Gard. 3: t. 246. 1828. **TYPE**: *Diplocoma villosa* D. Don ex Sweet (= *Heterotheca inuloides* Cass., var. indeterminate)

Stelmanis Raf., Fl. Tellur. 2: 47. 1836. **TYPE**: *Stelmanis scabra* Rafinesque, nom. illeg. (= *Chrysopsis scabra* Ell., nom. illeg.; *Inula scabra* Pursh, nom. illeg.; *Inula subaxillaris* Lam., *Heterotheca subaxillaris* (Lam.) Britt. & Rusby)

Heterotheca sect. *Chaetactis* DC., Prodr. 5: 317. 1836. **TYPE**: *Heterotheca chrysopsidis* DC. (= *H. subaxillaris* (Lam.) Britt. & Rusby)

Heterotheca sect. *Gymnactis* DC., Prodr. 5: 317. 1836. **LECTOTYPE** (designated here): *Heterotheca scabra* (Pursh) DC. (= *H. subaxillaris* (Lam.) Britt. & Rusby)

Under his sect. *Gymnactis*, DeCandolle included *H. inuloides*, *H. scabra*, *H. lamarckii*, and *H. leptoglossa*.

Plants of sect. *Heterotheca* are characterized by dimorphic achenes — disc achenes are compressed, strigose to sericeous, with a well-developed pappus; ray achenes are 3-angled, smaller, glabrous or much less pubescent, and completely epappose or rarely with a few short bristles or a minute corona. Phyllaries often are distinctly keeled. It is the only group of *Heterotheca* where an annual duration has evolved, and the plants tend to be erect from the base. Mostly following Wagenknecht (1960), Semple (1996) recognized 7 species and 4 non-typical varieties — the 8 species recognized here form a considerably different set. Most of the diversity in sect. *Heterotheca* occurs in Mexico and was described in an earlier study (Nesom 1990), but here entities previously treated at varietal rank within *H. inuloides* are recognized as species, *H. psammophila* is recognized as distinctive, and a previously undescribed species is recognized. Morphological distinctions between species are relatively small (as in other goldenaster species groups), but the geographic boundaries generally appear to be sharply defined.

1. HETEROTHECA SUBAXILLARIS (Lam.) Britt. & Rusby, Trans. New York Acad. 7: 10. 1887. *Inula subaxillaris* Lam., Encycl. Meth. Bot. 3: 259. 1789. **TYPE**: **USA**. Protologue: "Croît dans la Caroline, le Maryland, & peut-être dans d'autres parties de l'Amérique septentrionale." (probable holotype: P, not seen).

Wagenknecht (1960, p. 73) noted that "Lamarck's (1789) description is somewhat vague and on its own would scarcely distinguish this species from several others in related genera. No indication is given as to where he acquired his specimen. The type specimen (P) bears only the notation "Walter, Carolina" and the reference to the Plukenet plate."

Inula punctata Muhl., Cat. 76. 1813 [nom. nud.; referred to by Elliott and deCandolle as a synonym of *Inula scabra* Pursh].

Inula scabra Pursh, Fl. Amer. Septent. 2: 531. 1814 [nom. illeg.; Pursh cited *Inula subaxillaris* Lam. as a synonym]. *Chrysopsis scabra* (Pursh) Ell., Sketch Bot. S. Carolina 2: 339. 1824 [1823]. *Heterotheca scabra* (Pursh) DC., Prodr. 5: 317. 1836. *Stelmanis scabra* (Pursh) Raf., Fl. Tellur. 2: 47. 1836.

Heterotheca lamarckii Cass., Dict. Sci. Nat. 21: 131. 1821 [nom. illeg.; Cassini cited *Inula subaxillaris* Lam. as a synonym]. *Chrysopsis lamarckii* (Cass.) Nutt., Trans. Amer. Philos. Soc. n.s. 7: 315. 1840.

Heterotheca chrysopsidis DC., Prodr. 5: 317. 1836. **TYPE**: **MEXICO**. **Coahuila**. Protologue: "in Mexico circa Saltillo januar. flor. legit cl. Berlandier ... v.s. comm. à cl. Berlandier." Saltillo, Jan 1828, *J.L. Berlandier 1368* (holotype: GDC; isotype: P 00742816; probable isotypes: P 00742813, P 00742814, NY 163188; possible isotype: GH 55886, right side). Digital images! of all collections. The holotype was annotated as such by Semple in 1984 — it shows a collection date of Jan 1828 from Saltillo and collection number of 1368. The isotype is similar. The probable isotypes have "1368" as collection number but show no date. The GH collection is labeled collection number "109," collected in Saltillo in Jan 1828.

Heterotheca latifolia Buckl., Proc. Acad. Nat. Sci. Philadelphia 13: 459. 1862. *Heterotheca subaxillaris* var. *latifolia* (Buckl.) Gandhi & Thomas, Sida Bot. Misc. 4: 110. 1989. *Heterotheca subaxillaris* subsp. *latifolia* (Buckl.) Semple, Sida 21: 759. 2004. **TYPE**: **USA**. **Texas**. Llano Co.: No other locality data, Jun 1861, *S.B. Buckley s.n.* (probable holotype: PH! digital image!).

Heterotheca latifolia var. *petiolaris* Benke, Rhodora 30: 201. 1928. **TYPE**: **USA**. **Texas**. Galveston Co.: Galveston, 12 Mar 1928, *H.C. Benke 4585* (holotype: F digital image!).

Heterotheca subaxillaris var. *procumbens* Wagenk., Rhodora 62: 75. 1960. **TYPE**: **USA**. **Alabama**. Mobile Co.: ca. 1 mi SW of Dauphin Island Post Office, flattish dunes, 29 Jul 1940, *R.M. Harper 3801* (holotype: GH digital image!; isotypes: F digital image!, MO! digital image!, PH! digital image!, US digital image!).

Heterotheca latifolia var. *macgregoris* Wagenk., Rhodora 62: 103. 1960. **TYPE**: **USA**. **Kansas**. Morton Co.: 9 mi N of Elkhart, bluffs along Cimarron River, dry sandy prairie, 27 Aug 1951, *R.L. McGregor 5163* (holotype: KANU!).

Heterotheca latifolia var. *arkansana* Wagenk., Rhodora 62: 105. 1960. **TYPE**: **USA**. **Arkansas**. Logan Co.: Magazine Mountain, 10 Sep 1930, *D.M. Moore 30142* (holotype: TEX!).

Annual or biennial; herbage drying green, erect to decumbent or procumbent. Upper cauline leaves usually at least slightly subclasping, becoming reduced in size but mostly remaining ovate; phyllaries densely glandular, usually without non-glandular hairs, innermost 5–8 mm long; disc corollas glabrous or nearly so; ray achenes usually completely glabrous, disc achenes usually with 1–3 resinous veins; outer pappus strongly developed. Chromosome number, $2n = 18$ (many counts).

Within what is treated here as *Heterotheca subaxillaris*, Wagenknecht (1960) recognized *H. latifolia* and *H. chrysopsidis* as segregates at specific rank. Geographic trends can be observed and plants sometimes may be suspected of having originated in certain geographic areas, but plants occurring in broad areas of intergradation appear to be as numerous as those with names and said to have a distinctive combination of traits (see comments by Nesom 1990).

Semple (1996) recognized *Heterotheca subaxillaris* and *H. latifolia* as distinct species but later (2006) treated the same entities as subspecies — subsp. *subaxillaris* characterized as "Habit erect to procumbent, to 1 m tall; stem scabrous; lower leaf surfaces scabrous; phyllaries with a well-defined subapical tuft of short, thick hairs; outer coastal plain of SE US into northeastern Mexico." Burk (1961), however, found evidence that features of the coastal plain form are produced in response to environmental conditions. He transplanted North Carolina plants from a barrier island (Bogue

Barrier) and from an inland habitat to a common garden on the piedmont, where they "developed into virtually identical sets of plants." Using cloned individuals, he also observed that vestiture was significantly modified depending on the season and whether the plants were grown in a greenhouse or outdoors. Harms (1965) also documented the ease of environmental modification among plants of *H. subaxillaris*.

Burk also noted on the barrier island that most populations flowered in later summer and early fall but that one population flowered year-round. In January 1960, plants of the latter were in full flower while the others on the island were in winter-rosette form. In greenhouse experiments, he found that plants of the common winter-rosette form required long days to flower, while those flowering in January flowered under both long-day and short-day conditions. This difference in phenology has not been reflected in taxonomic proposals.

The name *Heterotheca chrysopsidis* has been applied to plants from Coahuila and adjacent Nuevo León that have woodier roots (perennial?) and shorter stature, petiolate, prominently thickened leaves (similar to coastal variants of *H. subaxillaris*), and deep reddish-brown pappus. These features are most pronounced in plants from gypseous areas of Nuevo León but intermediates are numerous.

2. HETEROTHECA GRANDIFLORA Nutt., Trans. Amer. Philos. Soc. n.s., 7: 315. 1840. **TYPE**: **USA. California**. Label: "Santa Barbara, in rupibus," [1836], *T. Nuttall s.n.* (holotype: BM digital image!).

Heterotheca floribunda Benth., Bot. Voy. Sulphur, 24. 1844. **TYPE**: Protologue: "San Pedro and San Quentin," no specimen cited (holotype: K?).

Along the Pacific coast, H.M.S. Sulphur visited the ports of San Pedro (Los Angeles Co., California) and San Quentin (Baja California) in October 1839. Bentham's description of *H. floribunda* is very brief and hardly diagnostic but Hall (1907), Wagenecht (1960), and others, followed here, have placed the name as a synonym of *H. grandiflora*.

Annual to biennial or short-lived perennial, plants to 2 m tall; stems and leaves sparsely to densely hispid-pilose to villous, herbage with a strong tendency to dry with a pronounced dark cast. Cauline leaves broadly lanceolate to triangular-lanceolate, narrowed to a sessile or subsessile, non-clasping, attenuate base, at least on the distal stems and commonly becoming linear-lanceolate to linear bracts. Phyllaries distinctly keeled (Fig. 3), with only glandular hairs or glandular and sparsely strigose, usually purple-tipped, innermost 7–9 mm long. Disc corollas prominently hairy on the throat. Ray achenes minutely strigose at least on the angles and commonly on the faces as well; pappus with a weakly developed outer series of scales or bristles. Chromosome number, $2n = 18$ (many counts).

These are tall plants with large heads, broadly lanceolate to triangular-lanceolate leaves with a non-clasping base and acute apex. The leaves usually are densely villous and the herbage usually dries with a dark cast. Pappus tends to be reddish brown. With its distinctive habit and achene morphology, it rarely is misidentified — small plants have been identified as *H. subaxillaris*, but the leaves with non-clasping base and relatively dense vestiture usually are diagnostic.

Heterotheca grandiflora is native in California and Baja California, introduced in Arizona, Utah, and Hawaii. Common on sandy or disturbed soils at altitudes from sea level to 2000 feet.

Figure 3. *Heterotheca grandiflora*, from BM holotype. Reddish brown pappus and strongly keeled phyllaries.

3. HETEROTHECA PSAMMOPHILA Wagenk., Rhodora 62: 76. 1960. **TYPE**: **USA**. **Arizona**. Yavapai Co.: 1 mi S of Sedona, sandy soil along edge of roadside ditch, 23 Aug 1957, *B.L. Wagenknecht 4824* (holotype: KANU, not located). **EPITYPE** (designated here): **Arizona**. Yavapai Co.: 0.5 km downstream from Granite Creek confluence and headwater springs of the Verde River, ca. 2.4 km upstream from Campbells Ranch, 4.7 km SE of Paulden, 1290 m, below an eroded terrace on the bank of the Verde River, roots partially in damp, gravelly soil with *Salix*, *Populus*, *Fraxinus*, *Baccharis*, 25 Jun 2011, *F.S. Coburn 336b* (ASU, Fig. 6).

Annual, thick-stemmed, up to 1.5(–2) m tall; stems and leaves sparsely to densely hirsute to hispid-pilose, herbage drying green, without a dark cast. Cauline leaves oblong to oblong-obovate, oblong-ovate, or triangular-ovate (commonly 3–4 times longer than wide, usually epetiolate and clasping to subclasping to nearly the base of the stem, vestiture reduced adaxially. Involucres 6–8(–9) mm high (innermost phyllaries); phyllaries densely glandular, without non-glandular hairs. Disc corollas glabrous or nearly so. Ray achenes usually completely glabrous; disc achenes usually with 1–3 resinous veins. Chromosome number, $2n = 18$.

Previously and through part of the current study, I treated *Heterotheca psammophila* as a synonym of *H. subaxillaris*, but further observations indicate there is rationale for its formal recognition. Such plants essentially are mostly restricted to Arizona, northern Sonora, and northwestern Chihuahua. Native populations edge into adjacent California and New Mexico.

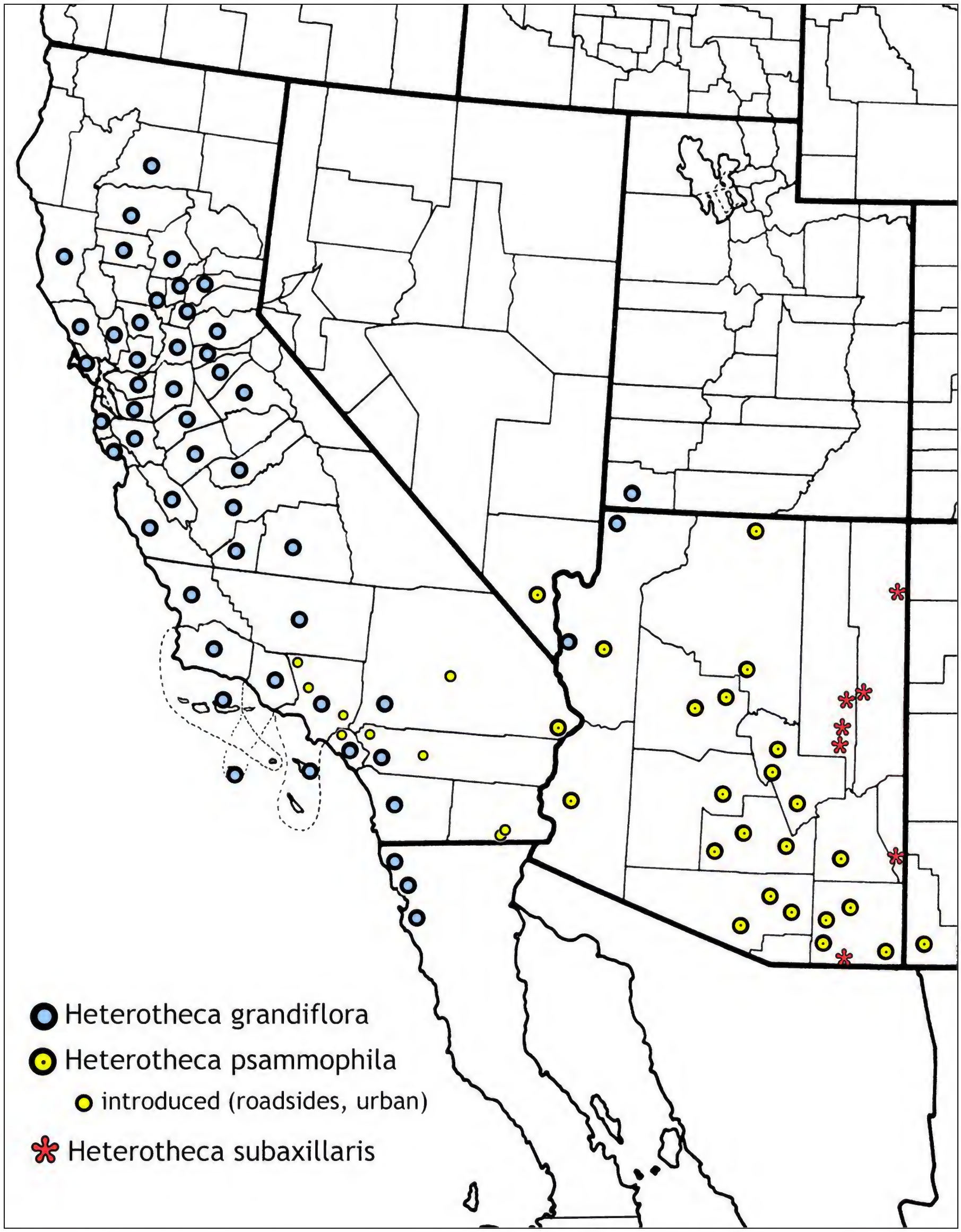

Figure 4. Distribution of *Heterotheca* sect. *Heterotheca*: *H. grandiflora*, *H. psammophila*, and *H. subaxillaris*.

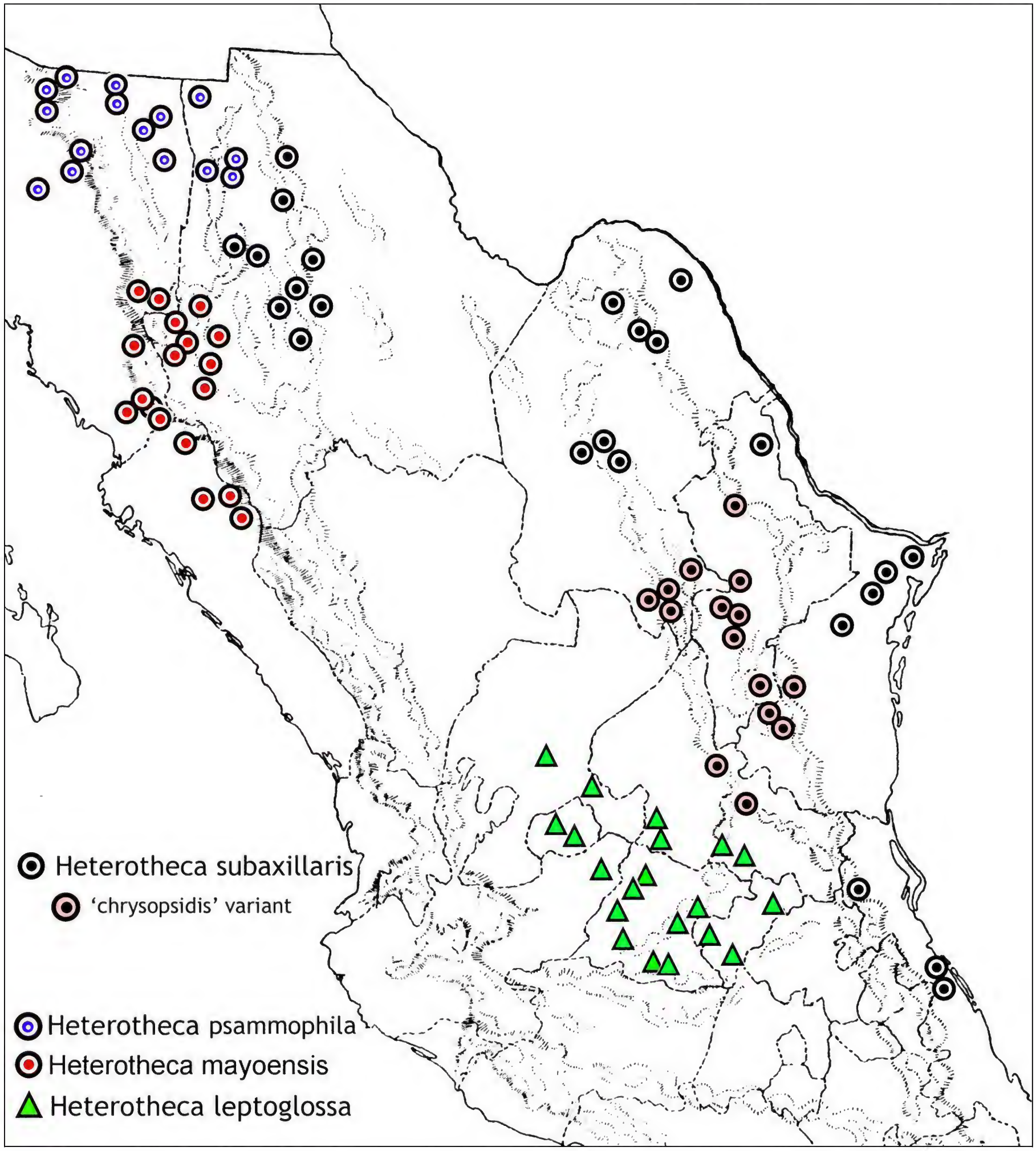

Figure 5. Distribution of *Heterotheca* sect. *Heterotheca*: *H. subaxillaris*, *H. psammophila*, *H. mayoensis*, and *H. leptoglossa*. *Heterotheca mayonensis* and *H. leptoglossa* also are shown in Figure 10, with the other Mexican endemics.

Figure 6. *Heterotheca psammophila*, epitype, *Coburn 336b* (ASU).

Figure 7. *Heterotheca psammophila*, Navajo Co., Arizona.

Figure 8. *Heterotheca psammophila*, Yavapai Co., Arizona.

Figure 9. *Heterotheca psammophila*, near Colonia Juárez in northwestern Chihuahua.

Representative collections of native *H. psammophila* in the USA outside of Arizona. California. San Bernardino Co.: Whipple Mts, along Colorado River at Big River SW of Earp, riparian woodland, sandy soil near river, 15 Nov 1980, *Sanders 2043* (UC, UCR). **New Mexico**. Hidalgo Co.: *Alford s.n.* (DES), *Dittmer 8575* (UNM), *Makings 3084* (DES), *Makings 3567* (TEUI), *Wagner 1391* (UNM), *Wagner 1678* (UNM), *Zimmerman 2274* (DES). Typical *Heterotheca subaxillaris* also occurs in Hidalgo Co.: *Dittmer 8574* (UNM), *Worthington 14879* (COLO).

Adventive populations of *Heterotheca psammophila* occur in southern California and perhaps in Brewster Co., Texas. Some California collections previously identified as *H. subaxillaris* have proved to be *H. psammophila* or *H. grandiflora* of small stature; all IDs of *H. subaxillaris* in California should be checked.

Collections of apparently adventive *H. psammophila*. California. Imperial Co.: Imperial Valley, ca. 10 mi E of El Centro, 13 Jun 1994, *Gruenhagen s.n.* (UCR, grown at UCR from field collection); 2 mi E of Calexico, border of California-Mexico, 7 Nov 1938, *Woglum 12645* (RSA). Los Angeles Co.: Irwindale, abandoned gravel pit adjacent to 210 Freeway, ca. 300 m E of Irwindale Ave, 31 Dec 1997, *Swinney 5890* (UCR); E Santa Susana Mts, Lyon Canyon area, W of I-5 Freeway, ca. 4 mi N of I-5/State Hwy 14 jct, 14 Jun 2004, *White 10498A* (UCR); SE Tehachapi Mts, Gorman area, Gorman Post Rd, scarce on roadside, 6 Jul 2006, *White 11608* (UCR). Orange Co.: Vicinity of city of Brea, immediately N of Carbon Canyon Rd and E of Placentia Ave, ca. 600 ft, heavily disturbed area, margin of *Quercus agrifolia* forest, 13 Oct 1992, *White 961* (UCR); city of Laguna Niguel, ridges and open slopes directly N of intersctn Crown Valley Pkway and Pacific Island Drive, 17 May 2004, *White 10383* (UCR). Riverside Co.: UCR campus, well-watered planter beside Boyce Hall, solitary weed, 23 Sep 1999, *Provance 1680B* (UCR); Indio, 2 mi S of Jackson St., sandy flat, 26 Sep 1965, *Roos s.n.* (RSA, UCR). **Texas**. Brewster Co.: Santa Helena Canyon, Big Bend National Park, *Moore & Steyermark 3467* (as cited by Wagenknecht: GH, PH, UC); near the mouth of Santa Helena Canyon, 8 Aug 1938, *Warnock T505C* (FSU, TEX).

In his key to species, Wagenknecht (1960, p. 66) distinguished *Heterotheca psammophila* by its "Stems up to 1.2 cm in diameter, the lateral branches coarse; leaves cordate-clasping, sparsely pilose above; phyllaries densely glandular and pilose." None of these features, however, is effective in identifying the form, at least as seen on herbarium specimens. A more consistent distinction is the morphology and vestiture of the cauline leaves — oblong to oblong-obovate, oblong-ovate, or triangular-ovate (commonly 3–4 times longer than wide), usually epetiolate and clasping to subclasping to nearly the base of the stem (vs. the proximal petiolate), and with reduced vestiture adaxially. *Heterotheca psammophila* produces larger heads than *H. subaxillaris* (innermost phyllaries 6–8(–9) mm long vs. 5–6(–7) mm) and they are generally taller and thicker-stemmed.

Semple (1996), following Wagenknecht, included *Heterotheca psammophila* in his key to species of sect. *Heterotheca*. For FNA in 2006, however, he treated it within the synonymy of *H. subaxillaris* subsp. *latifolia*, noting that "Robust plants (to 2 m) occurring in Arizona, New Mexico, and adjacent Texas have been treated as *Heterotheca psammophila*, but they grade into those treated as subsp. *latifolia* farther east on the prairies and eastward." I agree with Semple that plants with psammophila-like leaves and other features occur within the range of *H. subaxillaris*, particularly in the southeastern USA and in west Texas, but my assessment here of the taxonomy is weighted by the observation that the geographic range of *H. psammophila* appears to be sharply defined in both the USA and Mexico (Figs. 4, 5). Outlying variants in the USA are regarded here as populational variants within *H. subaxillaris*.

The *Heterotheca inuloides* group

Heterotheca inuloides has previously been treated inclusively. Wagenknecht (1960) treated *H. rosei* (in its initial description) as a variety of *H. inuloides*, noting its morphological distinction and (p. 70) that it "is geographically distributed in a manner to warrant its treatment as a variety." Some populational variants of *H. rosei* in the area of ne Nayarit-se Durango-sw Zacatecas and in the vicinity of Uruapan and Tancítaro, Michoacan, have inuloides-like vestiture and perhaps warrant formal recognition. *Heterotheca viridis* and *H. leptoglossa* were subsumed within *H. inuloides* without due consideration of their biology and geography. With numerous collections now available for study, these plants appear to comprise discrete entities in morphology and geography, identified as in the following key and including a newly described species.

In view of the geography, it would not be surprising to find that *Heterotheca subaxillaris* is evolutionarily sister to all the others or that *H. subaxillaris*, *H. psammophila*, and *H. grandiflora* as a group are sister to the Mexican endemics, which are identified here as the "*H. inuloides* group."

1. Outer phyllaries densely villous or hispid-pilose from base to tip with spreading to spreading-ascending, non-glandular hairs; perennial.

    2. Phyllaries usually distinctly purplish at least at the apices and commonly along the distal margins and midregion, hispid-pilose with thick-based, non-glandular trichomes ..... 7. **Heterotheca inuloides**
    2. Phyllaries completely without purple coloration, villous with thin-based non-glandular trichomes ..... 8. **Heterotheca viridis**

1. Outer phyllaries densely stipitate-glandular along the whole length, usually no or few non-glandular hairs or glabrous to strigose on the distal half with only fine and relatively thin-based glandular hairs; annual to biennial or perennial.

    3. Outer phyllaries completely glabrous to strigose along the distal midregion with appressed to ascending-appressed, fine and relatively thin-based, non-glandular hairs, eglandular to sparsely sessile-glandular distally or with short-stipitate glands near the phyllary apex, usually purple at the very apex ..... 6. **Heterotheca leptoglossa**
    3. Outer phyllaries densely stipitate-glandular along the whole length, usually without non-glandular hairs or the non-glandular hairs few.

        4. Annual or biennial; phyllaries without purple tips, stipitate-glandular sometimes with non-glandular hairs sparsely intermixed on the distal third ..... 5. **Heterotheca rosei**
        4. Perennial; phyllaries purple-tipped, stipitate-glandular and without non-glandular hairs ..... 4. **Heterotheca mayoensis**

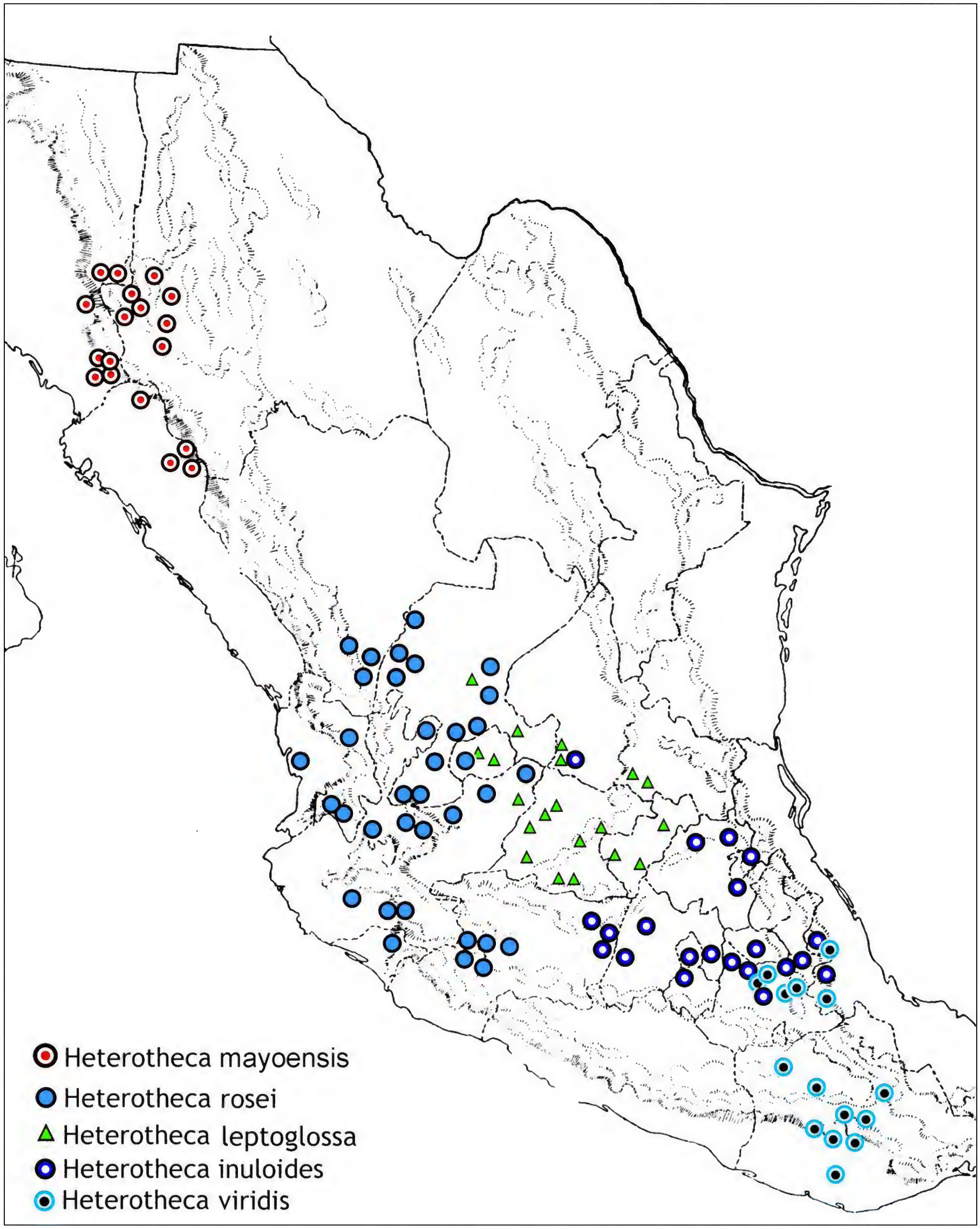

Figure 10. Distribution of Mexican endemics of sect. *Heterotheca* (the "*H. inuloides* group"): *H. mayoensis*, *H. rosei*, *H. leptoglossa*, *H. inuloides*, and *H. viridis*. *Heterotheca mayoensis* also is shown in Figure 5 with other species of northwestern Mexico.

4. HETEROTHECA MAYOENSIS Nesom, **sp. nov. TYPE**: **MEXICO**. **Chihuahua**. Mpio. Chinipas: Guicorichi, Rio Mayo, transition, slope of old milpa, 7 Oct 1935, *H.S. Gentry 1974* (holotype: MEXU 1356175 (Fig. 11); isotypes: MEXU 798554 (Fig. 12), MO (Fig. 13), PH!). The locality is at the western foot of Cerro Guicorichi, ca 9 km east of Loreto.

Distinct in its combination of oblanceolate to elliptic-oblanceolate leaves tapering to a narrow base, linear to filiform inflorescence bracts, stipitate-glandular phyllaries without non-glandular hairs, and its discrete, allopatric geographic range. Different from *H. subaxillaris* in its perennial duration, more elongate leaves, linear to filiform inflorescence bracts, smaller heads, and purple-tipped, stipitate-glandular phyllaries without non-glandular hairs. Different from *H. psammophila* in its perennial duration, mostly oblanceolate leaves tapering to a narrow base, and its discrete, allopatric geographic range. Most closely similar to *H. rosei* (see key and comments below).

Plants "perennial" (e.g., *Van Devender 93-1504*, *93-1401*; *Sanders 14278*; *Reina 96-376*), a "colonial weed" (*Gentry 6170*), "rhizomatous" (*Vega & Torres 1527*), from a thick, woody taproot that often elongates and perhaps appears like a rhizome. **Stems** 0.2–1 m tall, sparsely hirsutulous with fine, even-length hairs 0.5–1 mm long, eglandular to sparsely minutely stipitate-glandular, in the inflorescence becoming mixed hirsutulous and stipitate-glandular, peduncles (distal 2–4 cm) densely stipitate-glandular without non-glandular hairs. **Leaves**: proximal and mid narrowly oblong-oblanceolate to elliptic-oblanceolate or narrowly elliptic-oblanceolate to elliptic-oblong, 3.5–9(–10) cm long, blades 8–20 mm wide, basally attenuate to a distinct petiole or petiolar region, clasping to subclasping, sometimes with an abruptly widened flange at the petiole base, distal cauline becoming narrowly oblong and petiolate, margins entire or subentire to serrate with 3–7 pairs of teeth, surfaces sparsely villous-hirsute, minutely short-stipitate-glandular with orange glands on both surfaces but more densely so adaxially, margins minutely ciliate or without distinctly differentiated cilia. **Inflorescence** a cymosely branched corymb, peduncles bracteate; bracts linear to filiform. **Heads** 8–10 mm wide, phyllaries in 3–4 graduate series, linear-lanceolate, 0.5 mm wide, not keeled, longest (inner) 6–9 mm long, consistently purple-tipped. **Ray flowers** 20–25, corollas 10–12 mm long. **Disc corollas** ca. 5 mm long. **Achenes**: ray glabrous, disc sparsely strigose-sericeous. **Chromosome number**, $n = 9$ (count by D.J. Keil from *Lehto 19519*).

Flowering all year, perhaps most abundantly August-October. Tropical deciduous forest, oak, oak-pine, and pine forest, coniferous woods, clearings, roadsides, ruderal sites, fields, pastures, canyon bottoms; (400–) 700–1800 m.

Earlier (Nesom 1990) I noted that a population system in northwestern Mexico ("region a") might justifiably be formally regarded as a separate entity but treated the plants as part of the "psammophila" expression of *H. subaxillaris*. With formal recognition of *H. psammophila* as distinct and with a clearer definition of the geography (maps in Figs. 5 and 10) and morphology (Figs. 11-22) of the "region a" plants, they are here described as a distinct species.

In Chihuahua, where the range of *Heterotheca mayoensis* is nearly parapatric with that of H. subaxillaris, the two can be separate by the following couplet.

a. Perennial; non-glandular stem hairs 0.5–1 mm long; phyllaries purple-tipped, innermost 6–8(–9) mm long, stipitate-glandular and lacking non-glandular hairs, mid to upper cauline leaves narrowly oblong; inflorescence bracts linear to filiform ..... **Heterotheca mayoensis**

a. Annual; non-glandular stem hairs 0.5–2 mm long; phyllaries without purple tips, innermost 5–6(–7) mm long, sessile- to stipitate-glandular and almost always hirsute with non-glandular hairs, mid and upper cauline leaves ovate-lanceolate to oblong-lanceolate, inflorescence bracts lanceolate to ovate-lanceolate ..... **Heterotheca subaxillaris**

Heterotheca mayoensis is most closely similar to *H. rosei*, especially in its combination of vestiture and leaf morphology, and presumably part of the species group with geographic ranges restricted to Mexico. Compared to *H. mayoensis*, *H. rosei* has more slender taproots (presumably annual in duration), slightly larger heads, and distinctly larger stipitate glands. The two species are separated by more than 200 miles at their closest point.

***Heterotheca mayoensis*, additional collections**. **Chihuahua**. Mpio. Moris: Moris, Selva Baja Caducifolia, con encino, 700-1050 m, 29 Sep 1985, *Tenorio L. 10068* (MEXU); El Pilar, encino-pino alterado, 1400 m, 30 Sep 1985, *Tenorio 10079* (MEXU-2 sheets. Mpio. Temosachic: Nabogame, 1800 m, 5 Aug 1987, *Laferriere 674* (MEXU); Nabogame, 1800 m, 19 Aug 1987, *Laferriere 857* (MEXU); Nabogame, arroyo, 1800 m, 24 Oct 1988, *Laferriere 2187* (MEXU); Yepachic, abundant near stream, 1700 m, 18 Aug 1991, *Neff 8-18-91-8* (MEXU). Mpio. Urique: Sierra Tarahumara, Cuiteco, ruderal, 1732 m, Nov 2001, *Camou G. 516* (MEXU), *521* (MEXU). **Sinaloa.** Mpio. Badiraguato: Ocurahui, Sierra Surotato, pine forest area, ca. 6000-7000 ft, colonial weed about milpas, 27-30 Aug 1941, *Gentry 6170* (MEXU, NY, PH); Surutato a 5 km por la carretera a Santa Rita, Mesa del Fierro, bosque de coniferas, ca. 1800 m, Nov 28 1998, *Hernandez V. 1081* (MEXU); 1.4 mi NE El Cajon (11.3 mi NE Choix), dry sandy wash, 2100 ft, 25 Nov 1975, *Lehto 19519* [*n*=9, D.J. Keil 1975] (ASU); San Jose de los Hornos, 82 km NE de Mocorito camino a Surutato, bosque mixto de pino-encino, 1630 m, 2 Aug 1983, *Martínez 4191* (MEXU); 5 km SE de Surutato, 1650 m, bosque de encino, abundante, 22 Aug 1986, *Tenorio 11910* (MEXU, TEX); Surutato y alrededores, bosque de pino con presencia de *Acacia pennatula*, perturbado por actividades antrópicas, común, 1500 m, 9 Dec 2010, *Vega A. 11690* (MEXU); 11 km N de Surutato por la brecha Surutato-Santa Rita, llano entre claro de bosque, 2000 m, 9 Mar 1985, *Vega & Torres 1527* (MEXU). **Sonora.** Mpio. Alamos: Alamos, 17 Dec 1898, *Goldman 275* (NY); road N from Alamos to La Higuera, between Cerros El Cucurucho and El Aguaje, dry, short tree forest, with *Ipomea arborescens*, ca. 500 m, 29 Dec 1989, *Joyal 1345* (MEXU, TEX); Sierra Madre Occidental, Rancho Santa Barbara, Rio Cuchijaqui drainage, pastures and fields around ranch, ca. 1400 m, 17 Jul 1990, *Joyal 1490* (MEXU, TEX); San Bernardo, 26 Mar 1987, *López s.n.* (USON); El Caracol Trailer Park, ca. 10 mi W of Alamos on the road to Navajoa, flat weedy areas around the margins of the park, 400 m, 13 Dec 1988, *Sanders 8784* (TEX, UCR); 3 mi N of Rancho La Huerta (near the airstrip on the NW edge of Alamos) on the road to San Bernardo, tropical deciduous forest, uncommon, 2 Apr 1994, *Sanders 14278* (MEXU, UCR); 23 mi E of Navojoa on rd to Alamos, S side of road and roadcuts and on adjoining hills, 25 Feb 1967, *Sikes & Babcock 186* (TEX); 15 km E de Taymuco, 1400-1460 m, ecotono de selva baja caducifolia-encinar, 3 Oct 1985, *Tenorio 10169* (MEXU); Rancho La Sierrita (R. El Negrito), E slopes of the Sierra de Alamos, ca. 6 km (by air) SSW of Alamos, fallow field, 700 m, 26 Nov 1993, *Van Devender et al. 93-1401* (ASU, USON); ca. 1 km E of Mesa Colorada, disturbed roadside, 440 m, 12 Dec 1993, *Van Devender et al. 93-1504* (UCR, USON); 2 km WNW of Minas Nuevas on Alamos-Navojoa Road, N side of the Sierra de Alamos, roadside, 520 m, 27 Feb 1995, *Van Devender et al. 95-165* (USON); 5 km W of Las Chinacas on road from Las Tanques to Chinipas, cleared fields, originally pine-oak forest, 1500 m, 21 Aug 1991, *Yetman & Martin s.n.* (ARIZ). Mpio. Yécora: Yécora, Estanque del Arroyo de Yécora, entre el poblado de Yecora y las Cabañas Los Champiñones, bosque de pino y encino perturbado, frecuente en lugares arenosos, 1550 m, 4 Oct 1996, *Flores 4985* (USON); 5 km N of Tepustete, 1 Jan 1992, *Martin et al. s.n.* (ARIZ, MEXU); Yécora, abundant on flats near river, 17 Aug 1991, *Neff 8-17-91-1* (MEXU, TEX); Yécora, cerca del aserradero, 20 Aug 1991, *Reina s.n.* (USON); Yécora, a un lado de la pista, Yécora, 17 Sep 1991, *Reina s.n.* (USON); Yécora, near baseball field and cemetary, 1540 m, 6 Sep 1995, *Reina 96-376* (MEXU); Arroyo Hondo, 11.5 km E of El Kipur, 4 km W of Chihuahua border on Son 16, deep shady stream canyon with *Cupressus-Acer-Alnus* gallery forest, pine-oak forest on slopes, locally very common in rocky area in canyon bottom, 1460 m, 28 May 1996, *Reina 96-265* (MEXU); 8 km W of Yécora on Méx 16, Km 272 E of Cd. Obregón, 6 km E of Restaurant Puerto de la Cruz, 16 Aug 1997, *Trauba s.n.* (TEX); Yécora, arroyo in grassy field, 19 Aug 1997, *Trauba s.n.* (TEX); Yécora, 6 Oct 1995, *van Devender 95-731* (TEX); Arroyo El Otro Lado, Mesa El Otro Lado, 1-2 km NNE of Yécora on old road to Maycoba, pine-oak forest, edge of stream, 1520 m, 7 Sep 1995, *van Devender 95-811* (MEXU, TEX); Arroyo Hondo, 11.5 km E of El Kipur, 4 km W of Chihuahua border on Méx 16, shady canyon, 18 Jul 1997, *van Devender 97-882* (TEX).

Figure 11. *Heterotheca mayoensis*, Mpio. Chinipas, Chihuahua, holotype MEXU.

Figure 12. *Heterotheca mayoensis*, Mpio. Chinipas, Chihuahua, isotype MEXU.

Figure 13. *Heterotheca mayoensis*, Mpio. Chinipas, Chihuahua, isotype MO.

Figure 14. *Heterotheca mayoensis*, Mpio. Yécora, Chihuahua.

Figure 15. *Heterotheca mayoensis*, Mpio. Yécora, Chihuahua.

Figure 16. *Heterotheca mayoensis*, Mpio. Temosachi, Chihuahua.

Figure 17. *Heterotheca mayoensis*, Mpio. Urique, Chihuahua.

Figure 18. *Heterotheca mayoensis*, Mpio. Urique, Chihuahua.

Figure 19. *Heterotheca mayoensis*, Mpio. Badiraguato, Sinaloa.

Figure 20. *Heterotheca mayoensis*, Mpio. Badiraguato, Sinaloa. *Nash et al. L19519* (ASU).

Figure 21. *Heterotheca mayoensis*, Mpio. Badiraguato, Sinaloa. Heads from *Nash et al. L19519*, Fig. 20. Involucres and distal portion of peduncles stipitate-glandular, without other hairs.

Figure 22. *Heterotheca mayoensis*, Mpio. Alamos, Sonora. Heads from *Van Devender 1401*.

5. HETEROTHECA ROSEI (Wagenk.) Nesom, **comb. et stat. nov.** *Heterotheca inuloides* var. *rosei* Wagenk., Rhodora 62: 69. 1960. **TYPE**: **MEXICO**. **Jalisco**. 30 mi E of Guadalajara, grassland and roadsides, sandy soil, 25 Jul 1956, *B.L. Wagenknecht 2846* (holotype: KANU!; isotypes: F digital image!, MIN digital image!, NCU digital image!, NY digital image!).

Annual or biennial? from a woody taproot ("perennial … often flowering the first year, forming a short branched woody caudex" fide McVaugh 1984); phyllaries prominently stipitate-glandular and without non-glandular hairs or if present, the non-glandular hairs few and mostly on the distal third, usually with a prominent, raised keel on the proximal half.

In addition to a paucity or lack of non-glandular hairs, the phyllaries of *Heterotheca rosei* usually lack purple coloration or have only purplish margins, they are more densely stipitate-glandular than in typical *H. inuloides*, and the glands usually have thicker stipes. Judging from their more slender taproots, these plants are perhaps more short-lived than those of *H. inuloides*. These entities are morphologically distinct and geographically separate (non-overlapping).

Figure 23. *Heterotheca rosei*, heads from F isotype, Jalisco.

Figure 24. *Heterotheca rosei*, Jalisco.

Figure 25. *Heterotheca rosei*, Jalisco.

Figure 26. *Heterotheca rosei*, Jalisco.

6. HETEROTHECA LEPTOGLOSSA DC., Prodr. 5: 317. 1836. *Heterotheca inuloides* var. *leptoglossa* (DC.) Cook & Semple, Botany (Ottawa) 86: 892. 2008. **LECTOTYPE** (Semple 2008, p. 892): **MEXICO**. **Guanajuato**. Mexique (Leon à l'ouest de Guanajuato), 1827, *J. Mendez s.n.* (G-DC G00455695 digital image!; isolectotypes: G-DC G00455696 digital image!, GH digital image!). Protologue: "in Mexico prov. Leonina ad occid. urbis Guanaxuato legit cl. Mendez."

Annual to biennial or short-lived perennial, from a slender, woody taproot; phyllaries (outer series) completely glabrous to strigose along the distal midregion with appressed to ascending-appressed, fine and relatively thin-based, non-glandular hairs, eglandular or the non-glandular hairs mixed with sparse sessile glands distally or the glands short-stipitate near the phyllary apex, usually purple at the very apex, phyllaries not keeled. $2n = 18$.

McVaugh (1984) included *Heterotheca leptoglossa* within his concept of *H. inuloides* var. *rosei*, but *H. leptoglossa* appears to be isolated from both *H. rosei* and typical *H. inuloides*. There is no unambiguous evidence of intergradation between *H. leptoglossa* and *H. inuloides* where their ranges are contiguous or slightly sympatric. *Heterotheca leptoglossa* and *H. rosei* are sympatric in Aguascalientes, Zacatecas, and northern Jalisco apparently without significant intergradation.

Heterotheca rosei differs from *H. leptoglossa* in its less strongly woody taproots (and presumably shorter duration) and in its phyllaries densely glandular with long, thick-stiped glands and without purple-tips. The non-glandular hairs of *H. rosei* (if present) are usually erect or ascending, in contrast to the appressed ones of *H. leptoglossa*.

7. HETEROTHECA INULOIDES Cass., Dict. Sci. Nat. 51: 460. 1827. **TYPE**: **MEXICO**. No other data (probable holotype: FI, Herb. Webbianum ex Herb. Desfontaines, digital image!, photo-GH!).

"According to Cassini, this plant [the probable holotype] was said by Desfontaines to have originated in Mexico, sent by de Candolle from Geneva to the Jardin du Roi (presumably in Paris). The sheet at FI was annotated in Cassini's hand as 'Heterotheca inuloides, H. Cass.' There is in G-DC (fiche!) a very similar specimen noted as from 'J. de Paris 1828' that is possibly a duplicate of the type" (Nesom 1990).

Perennial; outer phyllaries densely stipitate-glandular in understory with thick, multicellular hairs, sparsely to moderately or densely villous-hirsute to hispid-pilose in overstory from base to tip with spreading to spreading-ascending, glassy, thick-based, non-glandular hairs.

8. HETEROTHECA VIRIDIS (Nesom) Nesom, **comb. et stat. nov.** *Heterotheca inuloides* var. *viridis* Nesom, Phytologia 69: 286. 1990. **TYPE**: **MEXICO**. **Oaxaca**. Distr. del Centro, Monte Alban, 1850 m, 14 Oct 1832, *C. Conzatti 4794* (holotype: LL!; isotype: MEXU).

Short-lived perennial from a thick woody taproot; phyllaries usually without purple coloration, moderately to densely villous along whole length with long, whitish, thin-based, non-glandular trichomes, surface minutely glandular, inner phyllaries often prominently keeled. Apparent intermediates between *Heterotheca viridis* and typical H. *inuloides* occur in northern Puebla and along the adjacent border with Veracruz where they are sympatric, but the zone of contact is narrow and intermediates are relatively few, in contrast to the much broader ranges where *H. inuloides* and *H. viridis* are distinct and consistent in morphology. Villarreal and Estrada (2016) mapped only *H. viridis* for Veracruz.

Figure 27. *Heterotheca viridis*, Oaxaca, *Kitchen 31* (ASU). Characteristic white-villous vestiture of involucres and peduncles.

HETEROTHECA SECT. AMMODIA (Nutt.) Harms, Castanea 39: 159. 1974. *Ammodia* Nutt., Trans. Amer. Philos. Soc. n.s. 7: 321. 1840. *Chrysopsis* sect. *Ammodia* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 6: 543. 1866. **TYPE**: *Ammodia oregona* Nutt. = *Heterotheca oregona* (Nutt.) Shinners.

Sect. *Ammodia* is characterized by a lack of ray flowers and an outer pappus of a few, very fine bristles 0.1–0.5 mm long (outer pappus in other sections is of relatively thick bristles or flattened scales, at least some of which are longer than 1 mm). All plants are perennial. The group is endemic to the Pacific coast region, occurring only in Washington, Oregon, and California. Semple et al. (1988) reported a diploid chromosome count for each of the four entities they recognized.

These taxa have generally been treated as varieties within a single species, beginning with Gray (1884), to Jepson (1901), Ferris (1960), Keck (1953), Munz and Keck (1959), and California treatments by Semple (1993 and subsequent). *Chrysopsis rudis* was described at specific rank by Greene (1894); it was treated at varietal rank without comment by Jepson (1901). Keck described var. *compacta* without any comment regarding its variability or interaction with other taxa.

Munz and Keck (1959) noted that the varieties "intergrade" but earlier botanists and contemporaries (e.g., Gray 1884; Jepson 1901; Ferris 1960) made no mention of their variability, nor can I find any such comment in regional California floras. Semple et al. (1988, p. 550, 551) observed that "Putative hybrids between pairs of the four varieties have been collected occasionally where sympatric. ... Intermediates collected represent about 10% of all herbarium specimens of the species

studied: 12 var. *oregona* x var. *rudis*, 2 var. *oregona* x var. *compacta*, 9 var. *rudis* x var. *compacta*, 5 var. *scaberrima* x var. *rudis*, and 9 var. *oregona* x var. *scaberrima*." Intergradation was not mentioned in the FNANM treatment of *Heterotheca* (Semple 2006).

In a multivariate analysis of the *Heterotheca oregona* complex, Semple et al. (1988) observed that "All four groups [taxa] were significantly different from one another ($\alpha = 0.005$)." Plots of 1st versus 2nd canonical variates (their Fig. 1) and 1st versus 3rd canonical variates (their Fig. 2) unambiguously separate the four taxa, except in Fig. 2, where var. *scaberrima* and var. *compacta* overlap. Following Semple's general concept of varietal taxa (see introductory comments above), Semple et al. treated each of the four at varietal rank. "The varietal differences are thought to have evolved as a consequence of geographic isolation" but "the ranges of the four races overlap to a great extent" and "the sympatric races now hybridize."

In the taxonomic summary here, *Heterotheca oregona*, *H. rudis*, and *H. scaberrima* are treated at specific rank. Plants identified as var. *compacta* by Semple and others appear to intergrade completely within more typical *O. rudis* and are not distinct from it in geography (see caveat below regarding the type of var. *compacta*).

1. Heads mostly scattered at ends of relatively long branches; leaves closely ascending, midcauline mostly 8–16 mm x 2–4(–5) mm, scabrous with only the multicelluar trichome bases or hispid to hirsute or strigose-hirsute, rarely without eglandular hairs ..... **Heterotheca scaberrima**
1. Heads in a loose corymboid cluster; leaves spreading to loosely ascending, midcauline (8–)15–30(–35) mm x 3–10 mm, vestiture various.

    2. Leaves completely without eglandular hairs, otherwise glandular to eglandular; stems minutely glandular, usually without eglandular hairs ..... **Heterotheca oregona**
    2. Leaves sparsely hirsute to hirsute-villous or hirsute-strigose, eglandular to glandular; stems often minutely glandular, usually villous to villous-hirsute ..... **Heterotheca rudis**

1. HETEROTHECA OREGONA (Nutt.) Shinners, Field & Lab. 29: 71. 1951. *Ammodia oregona* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 321. 1840. *Chrysopsis oregona* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 6: 543. 1866. **LECTOTYPE** (Semple 1987, p. 381): **USA**. **Oregon**. "Gravel bars of the Columbia & other tributaries," 1834, *T. Nuttall s.n.* (BM digital image!; isolectotypes: GH digital image!, PH!).

Semple et al. (1988) mapped the range of var. *oregona* as extending from northwestern Washington continuously southward to San Luis Obispo Co., California — almost completely sympatric in its California range with var. *rudis* (var. *oregona* extending further south in California than var. *rudis*). Semple's map shows var. *rudis* as restricted to California (except for a locality in Josephine Co., Oregon, possibly *Howell s.n.* [ORE] from near Waldo in 1887, or *Peirson 7012* [RSA] from the Rogue River gorge in 1926, both of which have vestiture that tends toward *H. rudis*). *Heterotheca oregona* is recognized here as a morphologically consistent entity of Washington and Oregon, occurring in California sporadically southward in a narrow extension immediately along the coast as far as Marin County and apparently sympatric with *O. rudis* in most of its California distribution. *Heterotheca rudis* is essentially restricted to California, its distribution northward ending abruptly in Humboldt and Siskyou counties (or possibly to southwestern Oregon — all specimens from ORE, OSU, and WILLU in the Oregon Flora Project database from Josephine, Curry, and Douglas counties are identified as *H. oregona* with *H. oregona* var. *rudis* as a synonym). I have not seen a record of *H. rudis* from Del Norte Co. California, where *O. oregona* has been abundantly collected.

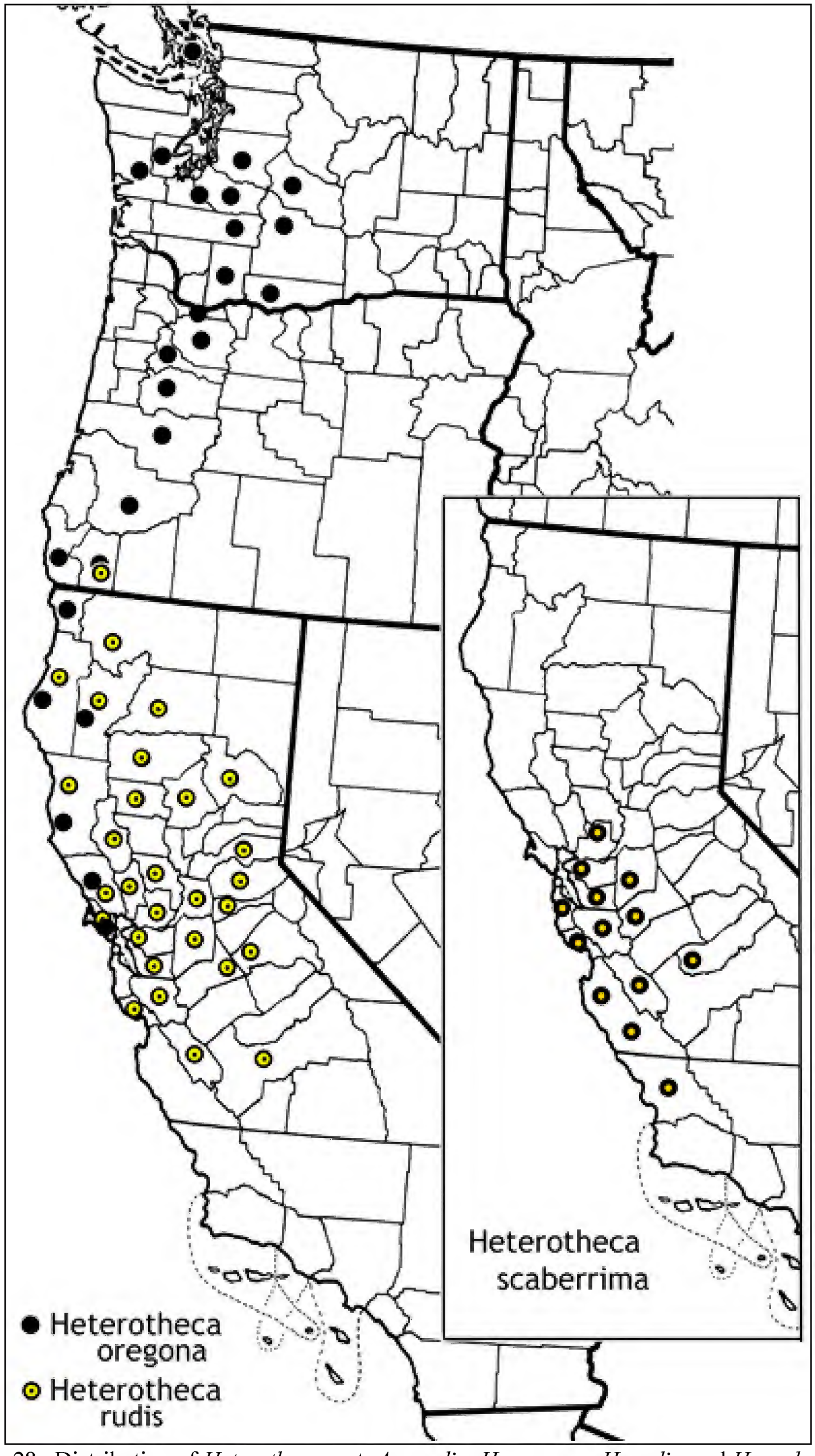

Figure 28. Distribution of *Heterotheca* sect. *Ammodia*: *H. oregona*, *H. rudis*, and *H. scaberrima*.

Figure 29. *Chrysopsis oregona* var. *compacta* holotype (identified here as *Heterotheca rudis*, see text).

2. HETEROTHECA RUDIS (Greene) Nesom, **comb. nov.** *Chrysopsis rudis* Greene, Man. Bay Reg., 174. 1894. *Chrysopsis oregona* var. *rudis* (Greene) Jepson, Fl. W. Mid. Calif., 558. 1901. *Heterotheca oregona* var. *rudis* (Greene) Semple, Brittonia 39: 382. 1987. **LECTOTYPE** (Semple 1987): **USA**. **California**. [Napa Co.]: Calistoga, 29 Aug 1888, *E.L. Greene s.n.* (NDG 53935 digital image!).

Chrysopsis oregona var. *compacta* Keck, Aliso 4: 102. 1953. *Heterotheca oregona* var. *compacta* (Keck) Semple, Brittonia 39: 382. 1987. **TYPE**: **USA**. **California**. Glenn Co.: Plentiful in dry gravelly stream bed near Newville, *Quercus douglasii* belt, 15 Oct 1922, *A.A. Heller 13736* (holotype: NY digital image!; isotypes: DS digital image!, MO digital image!, US digital image!, WTU!).

Heterotheca rudis characteristically has hairy (non-glandular) stems and leaves, and leaf size is more variable than in typical *H. oregona.* Most of the variability previously attributed to hybridization in the *H. oregona* complex instead appears to be infraspecific variation within *H. rudis*. The distinction between *H. rudis* and typical *H. oregona* is primarily in vestiture, but the discontinuity appears to be sharply delimited.

In 1988 (p. 556), Semple et al. observed that var. *compacta* is smaller in stature and has a relatively narrow capitulescence and smaller heads than the other taxa of sect. *Ammodia.* The type collection of var. *compacta* is a small plant and with relatively small leaves with densely strigose-villous to villous-hirsute vestiture (Fig. 5), but, as interpreted here, it appears to represent an extreme variant. In the present view, *compacta*-like variants intergrade with *Heterotheca rudis* sensu stricto in habit, leaf and inflorescence morphology, and vestiture. Semple et al. (1988) mapped var. *compacta*

and var. *compacta*-like variants as sympatric and almost perfectly congruent in geography with var. *rudis*. On the other hand, the striking appearance of the *H. compacta* type and the collector's description of it as "plentiful" suggests that the type locality should be reinvestigated, especially since serpentine is common in the Newville area.

3. HETEROTHECA SCABERRIMA (A. Gray) Nesom, **comb. et stat. nov.** *Chrysopsis oregona* var. *scaberrima* A. Gray, Synopt. Fl. N. Amer. 1(2): 124. 1884. *Heterotheca oregona* var. *scaberrima* (A. Gray) Semple, Brittonia 39: 383. 1987. **TYPE**: **USA**. **California**. Tulare Co.: Dry creek, Soledad, [no date], *J.W. Congdon s.n.* (holotype: GH digital image!).

Heterotheca scaberrima is distinct in morphology and has a relatively narrow geographical range, largely sympatric with *H. rudis* — few if any intermediates apparently are formed where the two occur together. *Heterotheca scaberrima* is treated here at specific rank, distinguished in the key above and as emphasized in the following comments by Semple et al. (1988, p. 557): "Variety *scaberrima* is the most distinctive of the species. The combination of small, coarsely scabrous, densely glandular leaves ... and densely glandular involucres with small outer phyllaries ... give the plants a readily recognizable appearance. The branches tend to be longer on average and the capitulescence is thus rather large and open compared to undamaged plants of the other varieties. Damage to the terminal meristem or procumbent orientation will result in elongation of the branches in all varieties giving a general appearance like undamaged plants of var. *scaberrima*. The leaves of secondary and tertiary branches are reduced in the species."

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STUDIES OF NEOTROPICAL COMPOSITAE–XIV. *BISHOPANTHUS WERFFII* (LIABEAE), A NEW SPECIES FROM CHACHAPOYAS, PERU

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ABSTRACT

The genus *Bishopanthus* H. Rob. (Compositae: Liabeae: Liabinae) has been rediscovered near Chachapoyas (Amazonas, Peru) and is expanded here to include a second leafy-capitulate species, ***Bishopanthus werffii*** Pruski & R. Ortiz., **sp. nov.** Key distinguishing features of the new species are opposite trinerved smooth leaves connected by tubular to cupular sheaths, paucicephalous capitulescences of yellow-flowered radiate capitula, and herbaceous-tipped obgraduate phyllaries. A key to the two species of *Bishopanthus*, a distribution map, and microscopic images of critical features of B. *werffii* are given. A table listing distinguishing characters of north Peruvian Liabeae with sheathing leaf bases is provided.

The genus *Bishopanthus* H. Rob. (Compositae) is a shrub belonging to tribe Liabeae (subtribe Liabinae), and is endemic to northern Peru. The generitype *Bishopanthus soliceps* H. Rob. was collected and photographed (Fig. 1) in January 1983, but only the poor fragmentary holotype sheet remains from the original duplicates. *Bishopanthus* was collected too late for inclusion in the then-in-press generic review of tribe Liabeae (Robinson 1983a: April). Shortly after collection, this material was described as a new genus and species, *B. soliceps* (Robinson 1983b: September), and placed in subtribe Liabinae. The microcharacters of *B.werffii*—linear, mid-sized style branches (Fig. 8A) and short-hexagonal pericarp raphide crystals (Fig. 9B)—support placement of *Bishopanthus* in subtribe Liabinae, as in Robinson (1983b). *Bishopanthus* and most Liabeae are characterized by opposite discolorous leaves, yellow-flowered radiate capitula, papillose style trunks, style branches with stigmatic surfaces continuous, and pappus mostly of elongate scabrous bristles. *Bishopanthus* is further distinguished by leaves with tubular to cupular sheathing bases, relatively few-capitulate capitulescences, herbaceous or at least herbaceous-tipped obgraduate phyllaries, and pale-anthers (Figs. 5–6).

Reports subsequent to Robinson (1983b) on chemistry (Singh et al. 1985) and pollen (Robinson & Marticorena 1986) of *Bishopanthus* were based upon the original material of *B. soliceps*. Because of the fragmentary nature of the type, *Bishopanthus* was not included in the key to

Peruvian Liabeae genera by Dillon and Sagástegui (1994). Recent keys to Peruvian Liabeae (Gutiérrez 2010) and genera of Liabeae (Robinson & Funk 2011), however, included *Bishopanthus*. Funk et al. (2013) provided a fine illustration of *B. soliceps*. Robinson (1983b) in the protologue cited *B. soliceps* as containing white latex, and Gutiérrez and Luna (2013) discussed the occurrence of latex in genera of tribe Liabeae.

Here we report that *Bishopanthus* was recollected near Chachapoyas (Fig. 2) in November 2012 by a team headed by Henk van der Werff (MO). The van der Werff plant is obviously a member of tribe Liabeae, a small tribe with its generic center of diversity in Peru. We were unsure, however, of the correct generic placement of the new species. We now have examined all genera of tribe Liabeae, and feel confident that *B. werffii* is correctly placed in *Bishopanthus*. The genus is thus expanded by us to include a newly described second species, *B. werffii*, typified by this recent collection from Chachapoyas. Although now ditypic, *Bishopanthus* remains a narrow-endemic known only from the environs of Chachapoyas (Depto. Amazonas, northern Peru). Similarly, monotypic *Holoschkuhria* H. Rob. (Compositae: Bahieae) was described as endemic to Chachapoyas, although it is now known also from adjacent Ecuador (Robinson et al. 2006).

Figure 1. Habit photograph of *Bishopanthus soliceps*, the generitype, showing bullate trinerved leaves and a solitary capitulum with about 27 ray florets. (About 20 km south of Chachapoyas at Tingo, *King & Bishop 9280*).

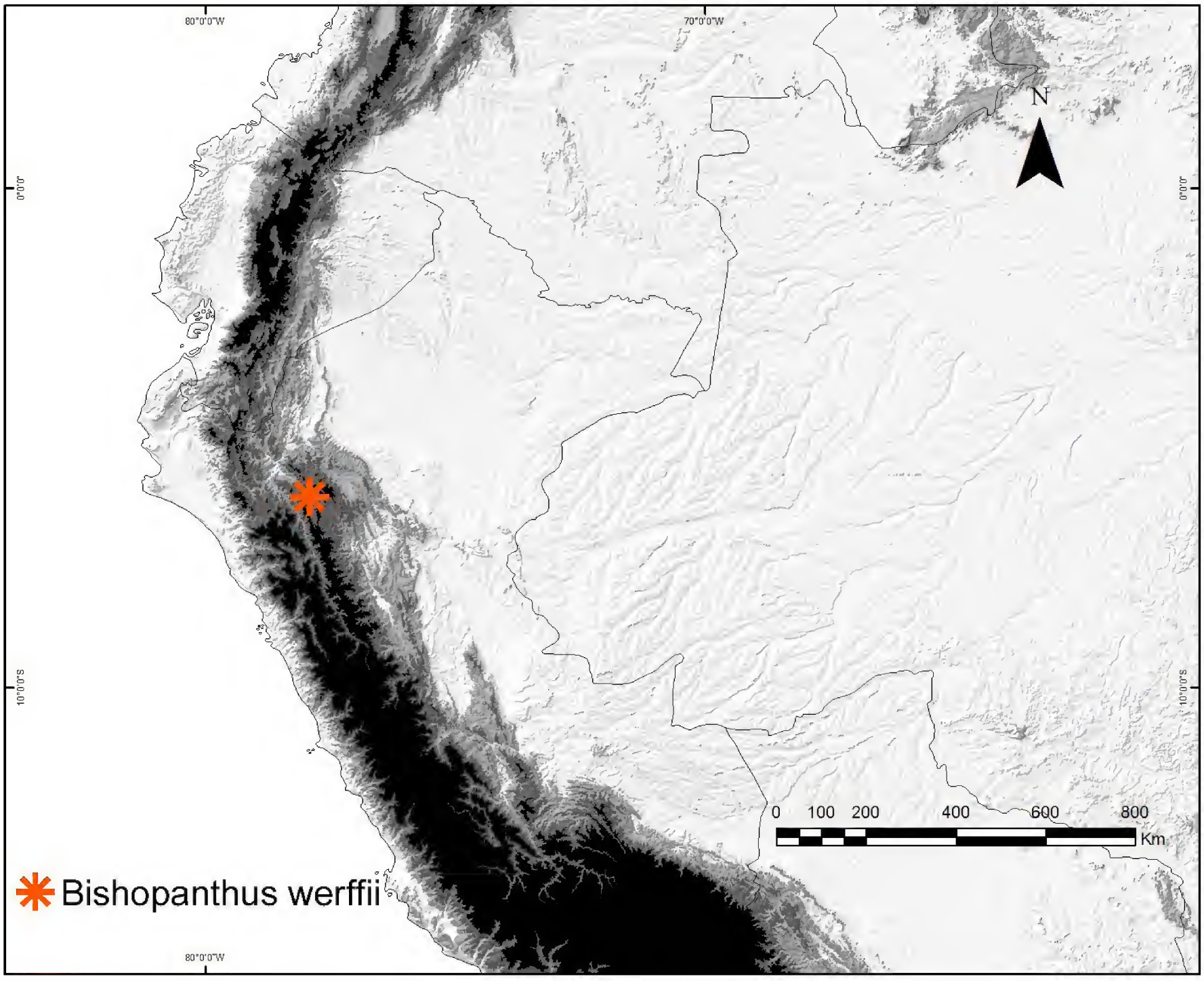

Figure 2. Distribution of *Bishopanthus werffii*, endemic to Chachapoyas in northern Peru. The generitype *Bishopanthus soliceps* is basically sympatric.

The most common genera of Liabeae are *Liabum* Adans. and *Munnozia* Ruiz & Pav. Both are widespread in throughout much of the Andes, as well as near Chachapoyas, Peru. Each contains species that are vining-shrubs or shrubby herbs that are mostly trinerved-leaved. On occasion *Liabum* and *Munnozia* may be perfoliate-leaved, but neither genus has sheathing (vaginate) leaf bases (Robinson 1983a), thereby differing from *Bishopanthus*. *Munnozia* further differs from most Liabeae by its black anthers. The segregate of *Munnozia*, paucispeciose, partly sympatric, bullate-leaved *Dillandia* V.A. Funk & H. Rob., similarly is perfoliate-leaved but lacks elongated sheathing leaf bases. *Pseudonoseris glandulosa* (Hieron.) Pruski, which includes in synonymy the generitype of Andean *Pseudonoseris* H. Rob. & Brettell (Fig. 3A), is a reddish-orange-flowered small herb, and thus differs from other regional Liabeae (Pruski 2012). Andean *Philoglossa* DC. differs from the new species by its herbaceous habit, concolorous leaves, and reduced pappus. None of the five aforementioned regional genera are overly similar to the new species, and none have basal leaf sheaths. Other Peruvian genera of Liabeae not closely resembling *Bishopanthus* include herbaceous *Chrysactinium* (Kunth) Wedd. and *Paranephelius* Poepp., and a few vining genera, e.g., *Oligactis* (Kunth) Cass.

The five regional genera of Liabeae that have sheathing leaf bases (viz Table 1) are *Bishopanthus* H. Rob. (now 2 spp.) (Figs. 1–2, 5–9), *Cacosmia* Kunth (3 spp.), monotypic *Chionopappus* Benth., *Erato* DC. (5 spp.) (Fig. 3B), and locally abundant *Ferreyranthus* H. Rob. &

Brettell (ca. 10 spp.) (Fig. 4). *Erato* (Paranepheliinae) sometimes has herbaceous-tipped outer phyllaries, but differs obviously from *Bishopanthus* by its long-petiolate leaves with strigose but concolorous, palmately veined, large orbicular blades. Peruvian *Chionopappus* (Paranepheliinae) is known only west of Río Marañón in the western Andean Cordillera, where it occurs mostly from Lima north to Cajamarca. *Chionopappus* is paucicephalous and has leafy outer phyllaries, thus resembling *Bishopanthus*, but *Chionopappus* differs from the aforementioned sheathing leaf based Peruvian Liabeae by reddish disk corollas and by plumose pappus bristles. *Cacosmia* (Liabinae) differs from other sheathing-leaved genera of Liabeae by its epappose 4–5-angled non-costate cypselae.

Figure 3. A. Capitulum of *Pseudonoseris glandulosa* (Hieron.) Pruski, showing graduated phyllaries, the reddish-orange ray corollas, and stipitate-glandular indument. B. Sheathing leaf bases of *Erato polymnioides* DC. (A Karajia near Chachapoyas, *Pruski & Ortiz 4893*; B Oxapampa, *Pruski et al. 4381*).

Figure 4. Diagnostic characters of *Ferreyranthus*. A. Sheathing (vaginate) leaf bases of bullate-leaved *Ferreyranthus rugosus* (Ferreyra) H. Rob. & Brettell. B. Flowering stem of *Ferreyranthus excelsus* (Poepp.) H. Rob. & Brettell group sensu Dillon and Sagástegui (1994), showing the many small capitula and the pinnately veined (as seen abaxially) smooth leaves. (A About 20 km west of Chachapoyas between Karajia and Quiocta, *Pruski & Ortiz 4872*; B About 20 km south of Chachapoyas between Tingo and Kuélap, Carlos Amasifuen, July 2018).

Table 1. Northern Peruvian genera of Liabeae having sheathing (vaginate) leaf bases.

Bishopanthus (Liabinae)	Leaf blades trinerved, discolorous, bullate or smooth; latex present in *B. soliceps*, possibly absent in *B. werffii*	Involucre with phyllaries obgraduate, outer phyllaries herbaceous-tipped; cypselae setose and glandular, with long scabrous pappus bristles
Cacosmia (Liabinae)	Leaf blades trinerved, discolorous, bullate; with or without latex	Involucre with phyllaries graduate, outer phyllaries scarious; cypselae glabrous, without pappus
Chionopappus (Paranepheliinae)	Leaf blades trinerved, discolorous, smooth; latex absent	Involucre with phyllaries obgraduate, outer phyllaries leafy; cypselae setulose, eglandular, with long plumose pappus bristles
Erato (Paranepheliinae)	Leaf blades palmatinerved, concolorous (but often strigose), smooth; latex present	Involucre with phyllaries graduate, outer phyllaries usually scarious; cypselae setulose or glabrous, eglandular, with long scabrous pappus bristles
Ferreyranthus (Liabinae)	Leaf blades pinnately veined, discolorous, bullate or smooth; latex absent	Involucre with phyllaries graduate, outer phyllaries scarious; cypselae setose and glandular, with outer squamellae and elongate scabrous inner pappus bristles

We initially thought that the new species could be a *Ferreyranthus* (Fig. 4), a genus (subtribe Liabinae) revised by Dillon and Sagástegui (1994). *Ferreyranthus* proves to be different than the van der Werff plant, however, by its pinnately veined leaves, large corymbiform-paniculate capitulescences, clearly graduated phyllaries, and outer pappus of moderately broad squamellae. Otherwise, *Bishopanthus* seems fairly similar to *Ferreyranthus*: they are the only elongate-pappose regional Liabinae genera with sheathing leaf bases (Table 1).

A footnote in Dillon and Sagástegui (1994) stated that they keyed Peruvian genera of Liabeae, except poorly known *Bishopanthus*. The first author examined the fragmentary holotype of *Bishopanthus* at the Smithsonian Institution in the 1990s during a nine-year residence there. The footnote noting the absence of *Bishopanthus* in the generic key by Dillon and Sagástegui (1994), triggered memory of the sheathing-leaf based plant and of its field photograph (Fig. 1), shown to the first author a few decades ago by Bob King and Harold Robinson.

We realized *B. werffii* had the essential characters—trinerved leaves joined by leaf sheaths, few capitula, large bracteate outer phyllaries, and narrow outer pappus bristles—of *Bishopanthus*, a genus previously known only from the type that is bullate-leaved and has moderately large monocephalous capitula. By these features we take the van der Werff plant, as the second species *Bishopanthus*, describing it here as *Bishopanthus werffii.* Henk van der Werff (pers. comm.) noted no latex in his collection, whereas *B. soliceps* reportedly contains latex. Latex characters, however, are sometimes known elsewhere to vary within individual genera of Liabinae (e.g., *Cacosmia*), but nevertheless we note that *B. werffii* may lack latex as does *Ferreyranthus*. Gutiérrez and Luna (2013) and Funk et al. (2011) noted that most taxa of subtribe Liabinae are characterized by absence of latex.

As redefined by the inclusion of *Bishopanthus werffii*, *Bishopanthus* still seems similar to *Ferreyranthus* (Liabinae sensu Robinson 1983a), especially to small-leaved *F. gentryi* H. Rob. and *F. vernonioides* (Muschl.) H. Rob. & Brettell. We follow Robinson (1983b) and use the trinerved leaves, few-capitulate branches, and outer leafy phyllary characters as diagnosing *Bishopanthus* and distinguish it from *Ferreyranthus*. Each *Bishopanthus* and *Ferreyranthus* have a shrubby habit,

sheathing leaf bases, and mid-sized disk floret style branches, and are thereby seeming related. *Ferreyranthus* also parallels the expanded *Bishopanthus* by being comprised of both bullate-leaved and smooth-leaved species (Fig. 4, Table 1). Acaulescent *Pseudonoseris* as well as other genera of Liabeae are also known to contain species with leaves either adaxially bullate or smooth (Robinson 1983a; Pruski 2012). The very striking bullate leaf character thereby appears not always to be generically diagnostic within Liabeae, but instead in the cases of *Bishopanthus*, *Ferreyranthus*, and *Pseudonoseris* only distinguishes species.

We note that *Munnozia* of subtribe Munnoziinae includes species with both pinnate-veined leaves and trinerved leaves, both monocephalous species and corymbiform-paniculate species, as well as species with either graduate to subequal or obgraduate leafy-bracteate phyllaries, features distinguishing *Bishopanthus* from *Ferreyranthus*. Although the leafy-bracteate outer phyllary character in some Compositae often seems to be influenced by environment (in simple terms, wetter areas may have a disproportionate high number of leafy bracted species), in the present case of partly sympatric *Bishopanthus* and *Ferreyranthus* the differences in the leafy-bracteate capitulum character may perhaps be phylogenetically informative, and not environmentally driven. *Bishopanthus soliceps* (as noted by Robinson 1983b) and *B. werffii* are very similar in gestalt to *Cacosmia* (Liabinae), which differs, however, by its much reduced pappus and few-flowered capitula. Even though an expanded *Bishopanthus* now becomes even more similar to the earlier *Ferreyranthus* than previously thought, while reviewing an early draft of our manuscript Liabeae authority Harold Robinson (pers. comm., 31 December 2013) said that our "placement" of the new species in *Bishopanthus* "is as good as any."

The purpose of the present note is to validate *Bishopanthus werffii*, to put its discovery into context, and to lay the ground work for further work on *Bishopanthus*, *Ferreyranthus*, and *Munnozia*. Our searches from April–July 2018 in mountains surrounding Chachapoyas resulted in documentation of several genera of Liabeae (e.g., Figs. 3–4), but not of *Bishopanthus*. Our failure to find the genus suggests that *Bishopanthus* is relatively rare, and also that it is now time to validate *Bishopanthus werffii.* We intend to further explore areas near Chachapoyas, however, hoping to find *Bishopanthus* and to sequence it; *Bishopanthus* was not sequenced in recent phylogenies (e.g., Soejima et al. 2008; Funk et al. 2012).

The two species of *Bishopanthus* are distinguished in the following key.

Key to species of *Bishopanthus*

1. Leaves bullate adaxially, blade margins denticulate nearly throughout; capitulescence solitary-capitulate; capitula (45–)49–53-flowered, ca. 10 mm tall; phyllaries recurved, abaxially bullate; ray florets (20–)24–29; disk florets ca. 25, corollas 7–7.5 mm long, hirtellous with patent trichomes proximally; anther appendage oblong-ovate, 0.4–0.5 mm long
.....**Bishopanthus soliceps** H. Rob.

1. Leaves nearly smooth adaxially, blade margins entire to few-denticulate with 1–3 teeth; capitulescence open-cymose-corymbiform; capitula 23–28-flowered, 8–9 mm high; phyllaries pressing straight , abaxially smooth; ray florets 11–13; disk florets 12–15, corollas 6.2–6.5 mm long, glabrous proximally, never setose; anther appendage lanceolate, 0.7–0.8 mm long
..... **Bishopanthus werffii** Pruski & R. Ortiz

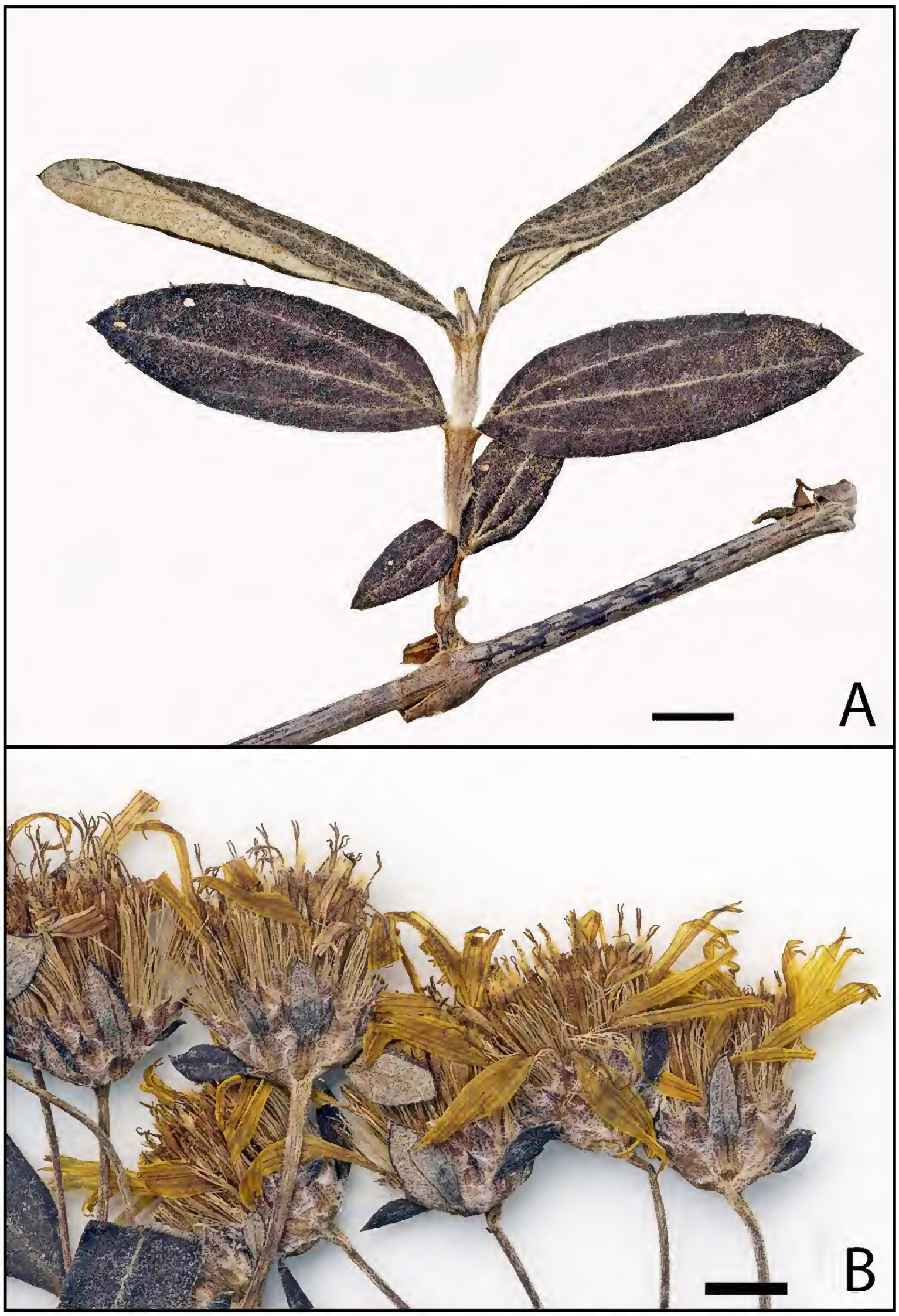

Figure 5. Close-ups of holotype of *Bishopanthus werffii*, showing generically important features. A. Branchlet showing nodes with sheathing-based trinerved smooth discolorous leaves. B. Capitula showing yellow ray corollas, pale anthers, and obgraduate phyllaries, the outer series of which is herbaceous distally. The capitula appear leafy-bracteate. (From the holotype, *van der Werff et al. 25642*, MO). Scale bars 5 mm.

BISHOPANTHUS WERFFII Pruski & R. Ortiz, **sp. nov. TYPE: PERU. Amazonas.** Along road from Utcubamba Valley to Luya and Karajia, degraded dry scrub, 6° 12' 08" S, 77° 54' 29" W, 2000–3000 m, 14 Nov 2012, *van der Werff, Valenzuela, Shareva & Reyes 25642* (holotype: MO; isotype: USM, one isotype to be distributed). Figures 2, 5–9.

Suffruticosa circiter 0.5 m alta; folia opposita brevipetiolata basaliter vaginata, lamina elliptico-lanceolata vel elliptica 1–4 × 0.5–1.4 cm chartacea trinervis discolorata supra virida laevis sparse arachnoideo-tomentosa et glandulosa, subtus ochracea arachnoideo-tomentosa et glandulosa; capitulescentia cymosa-corymbiforma 4–8 cm alta et lata, 20–40-capitulata, rami distaliter 4–5 cm longi 5-capitulati, pedunculi 0.7–3 cm longi tenui; capitula radiata 8–10 mm alta flosculis 23–28; involucrum campanulatum 5–6.5 × 5–7 mm; phyllaria 26–28 obgraduata dimorphica 3–4-seriata, externa herbacea distaliter arachnoideo-tomentosa apice reflexa, interna chartacea subglabrata erecta; flosculi radii 11–13, corollis 10–12 mm longis; flosculi disci 12–15 corollis 6.2–6.5 mm longis infundibuliformis basaliter glabrata nec setosa distaliter glandulosa, anthera circiter 3 mm longa pallida appendice lanceolata 0.7–0.8 mm longa, styli rami brevi; cypselae 1.5–1.7 mm longae setosae et glandulosae; setae internae pappo 5.3–5.8 mm longae.

Shrubs ca. 0.5 m tall, branching opposite (trichotomous); stems much-branched, subterete or slightly angled, loosely arachnoid-tomentose and sessile-glandular, possibly lacking latex, nodes sheathed in tubular to cupular (vaginate) leaf base that segments longitudinally in older stems, main stem internodes shorter than leaves, branches 12–22 cm long, ultimate flowering branchlets 4–5 cm long with 2–3 pairs of leaves and internodes about as long as leaves. **Leaves** with base moderately to strongly vaginate with lingering arachnoid-tomentulose and glandular sheath 1–4 mm long; petiole 0.1–0.2 cm long, broadly winged; blade elliptic-lanceolate to elliptic, 1–4 × 0.5–1.4 cm, chartaceous, trinerved from petiole, weakly reticulate with distal secondary and tertiary veins more or less equally thin, surfaces discolorous, adaxial surface mostly green, more or less smooth with midrib and basal pair of arching secondary veins only slightly impressed, never obviously bullate, lingering arachnoid-tomentulose (especially along the three main veins) and also moderately punctate-glandular, abaxial surface ochraceous, moderately arachnoid-tomentose but never so dense as to obscure underlying sessile glands, trichomes to ca. 0.5+ mm long, weakly flagelliform with slightly enlarged base, midrib and secondary veins visible and slightly raised but tertiary reticulation basically obscured by tomentum, base cuneate to obtuse, margins entire to few-denticulate with 1–3 teeth 0.2–0.4 mm long, sometimes slightly revolute, apex acute to obtuse, mucronulate. **Capitulescence** open-cymose-corymbiform, paucicapitulate, each main lateral flowering branch 4–8 cm long and broad, rounded in overall shape, each main lateral flowering branch 20–40-capitulate, ultimate flowering branchlets 4–5 cm long, each ultimate branchlet nearly at right angles to next higher order flowering branch, each usually flat-topped and 5-capitulate; peduncles 0.7–3 cm long, thin, moderately arachnoid-sericeous and sessile-glandular, sometimes 1–2-bracteolate immediately below capitulum by excurrent outer phyllaries. **Capitula** radiate, 8–10 mm tall, 23–28-flowered, appearing leafy-bracteate; involucre campanulate, 5–6.5 × 5–7 mm, much shorter than the disk florets but pressing with outer series of phyllaries almost as long as disk florets; phyllaries 26–28, obgraduate, dimorphic, 3–4-seriate; outer ca. 6 phyllaries oblong to spatulate or pandurate, 5–8 × 1.5–1.8 mm, usually somewhat spreading, straight, herbaceous or at least herbaceous-tipped, 3-nerved in proximal half, abaxially ochraceous, lingering arachnoid-tomentulose to glabrate proximally, arachnoid-tomentose in distal half, adaxially green, sparsely lingering arachnoid-tomentulose; inner 2–3 series of phyllaries moderately graduate, ovate grading to innermost lanceolate, 3–5 × 0.6–1.5 mm, appressed, chartaceous, stramineous, 3–5-nerved, subglabrous or with distal margin ciliolate or with apex sometimes lingering arachnoid-pubescent, apex acute to acuminate; clinanthium ca. 2 mm diam., spiculiferous, spicules 1–1.5 mm long, broad-based and abruptly narrowed or lacerate into sharp attenuate tips. **Ray florets** 11–13, pistillate; corolla 10–12 mm long, 3+0 (rarely 3+1 with tube ca. 3.5 mm long, inner lip ca. 3 mm long, limb ca. 6 mm long), yellow, tube 2.5–3 mm long, sparsely setulose, limb oblanceolate, 7.5–9 ×

1.2–1.6 mm, 5-nerved, apex 3-dentate, teeth 0.5–1 mm long; style well-exserted, branches linear, nearly as long as exserted portion of trunk, longer than those of disk florets. **Disk florets** bisexual, 12–15; corolla narrowly funnelform, 6.2–6.5 mm long (ca. 5.6 mm long when dry), 5-lobed, yellow, tube and throat not well-differentiated, somewhat glandular in distal 2/3, glands obovoid and minutely stalked, eglandular and glabrous, never setose, in proximal 1/3, tube, throat, and lobes subequal, tube 2–2.1 mm long, throat 2–2.1 mm long, throat only slightly ampliate, lobes lanceolate, 2.2–2.3 mm long; anthers 2.7–3 mm long, stramineous, filament glabrous, appendage lanceolate, 0.7–0.8 × ca. 0.2 mm, basal spurs 0.4–0.5 mm long; pollen spherical, echinate, tricolporate; style trunk long-papillose distally, branches 1–1.2 mm long, mid-sized, linear (not filiform), about as long as the exserted portion of long-papillose shaft, stigmatic surfaces continuous. **Cypselae** (immature) obconic, 1.5–1.7 mm long, 8–10-costate, brown, pericarp raphide crystals short-hexagonal, 10–15μm long (cypselae immature and perhaps crystals under-developed), surfaces moderately setose with patent biseriate duplex trichomes (twin hairs) 0.1–0.15 mm long, also moderately to densely sessile-glandular, carpopodium annular, 0.1–0.15 mm tall; pappus bristles ca. 30, 2–3-seriate, stramineous, scabrous, mostly subequal and 5.3–5.8 mm long but with a few outer narrow bristles (not broadened into squamellae) 1–1.5 mm long, the longer bristles of ray florets longer than corolla tube, the longer bristles of disk florets reaching to about proximal 1/3 of the corolla lobes.

Eponymy. We are pleased to name this species for our colleague Dr. Henk van der Werff (MO), collector of the type. Henk van der Werff is well-known for his work on the Flora del Río Cenepa, Amazonas, Perú, and as a specialist of Lauraceae, which are especially diverse at mid-elevations in the montane neotropics, such as where he discovered *B. werffii*.

Figure 6. Holotype of *Bishopanthus werffii* Pruski & R. Ortiz. (*Van der Werff et al. 25642*, MO). Scale bar 5 cm.

Figure 7. Florets of *Bishopanthus werffii*. A. Rays: anomalous 3+1 ray floret (left) with cypsela and pappus bristles removed; intact 3+0 ray floret (right). B. Three disks florets showing mid-sized style branches and proximally non-setose corollas; the cypsela and pappus bristles have been removed. C. Proximal portion of disk corolla with sparse glands and without patent trichomes. D. Anthers and style from disk floret showing lanceolate apical anther appendages (adaxial surfaces) (lower background) and papillose style (dark-staining and curving towards upper right). (From the holotype, *van der Werff et al. 25642*, MO). Scale bars A–B 5 mm, C 0.5 mm, D 1 mm.

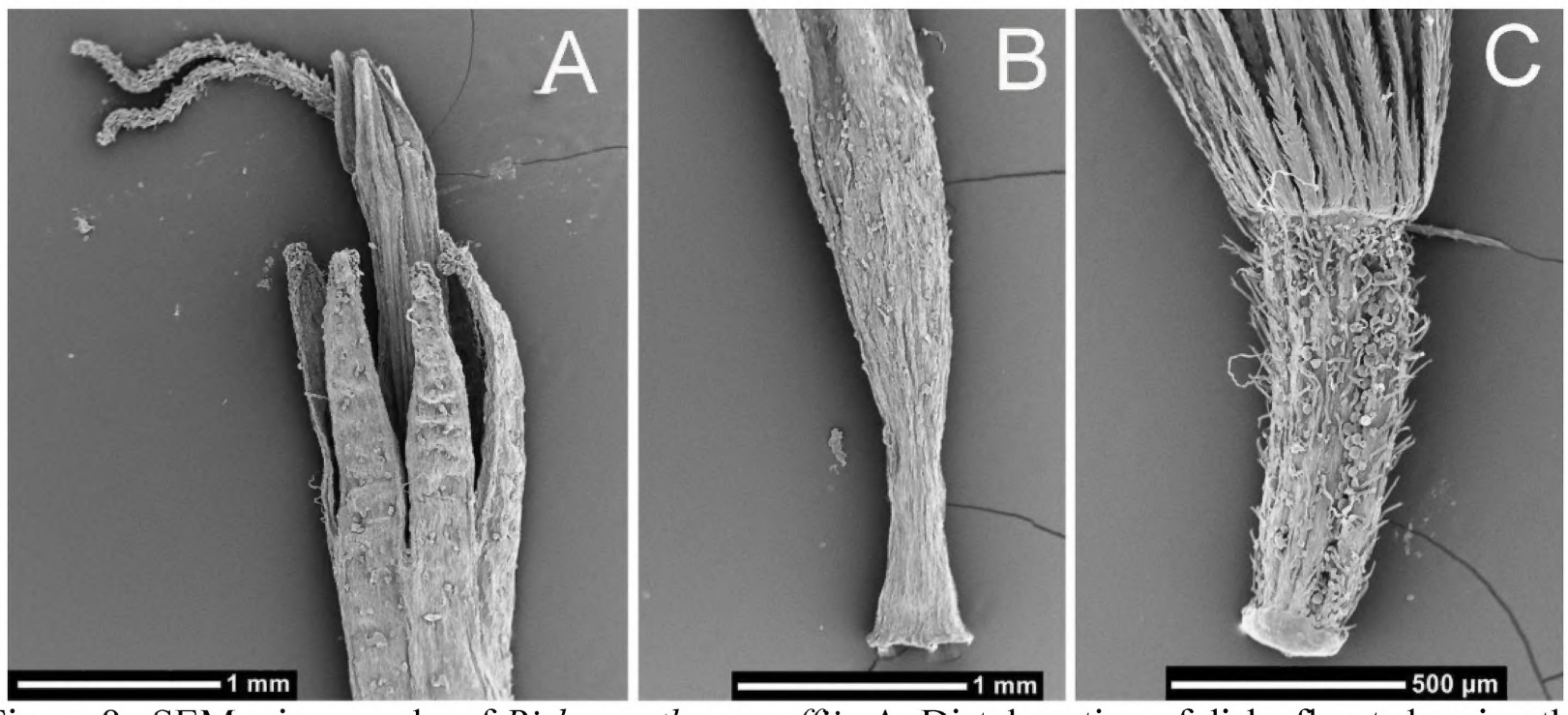

Figure 8. SEM micrographs of *Bishopanthus werffii*. A. Distal portion of disks floret showing the papillose style shaft and branches (upper left) and elongate corolla lobes and the mid-sized style branches B. Disk corolla throat and the glabrous tube. C. Cypsela showing setose and sessile-glandular indument, 8–10 ribs, and narrow, mostly elongate scabrid pappus bristles. (From the holotype, *van der Werff et al. 25642*, MO).

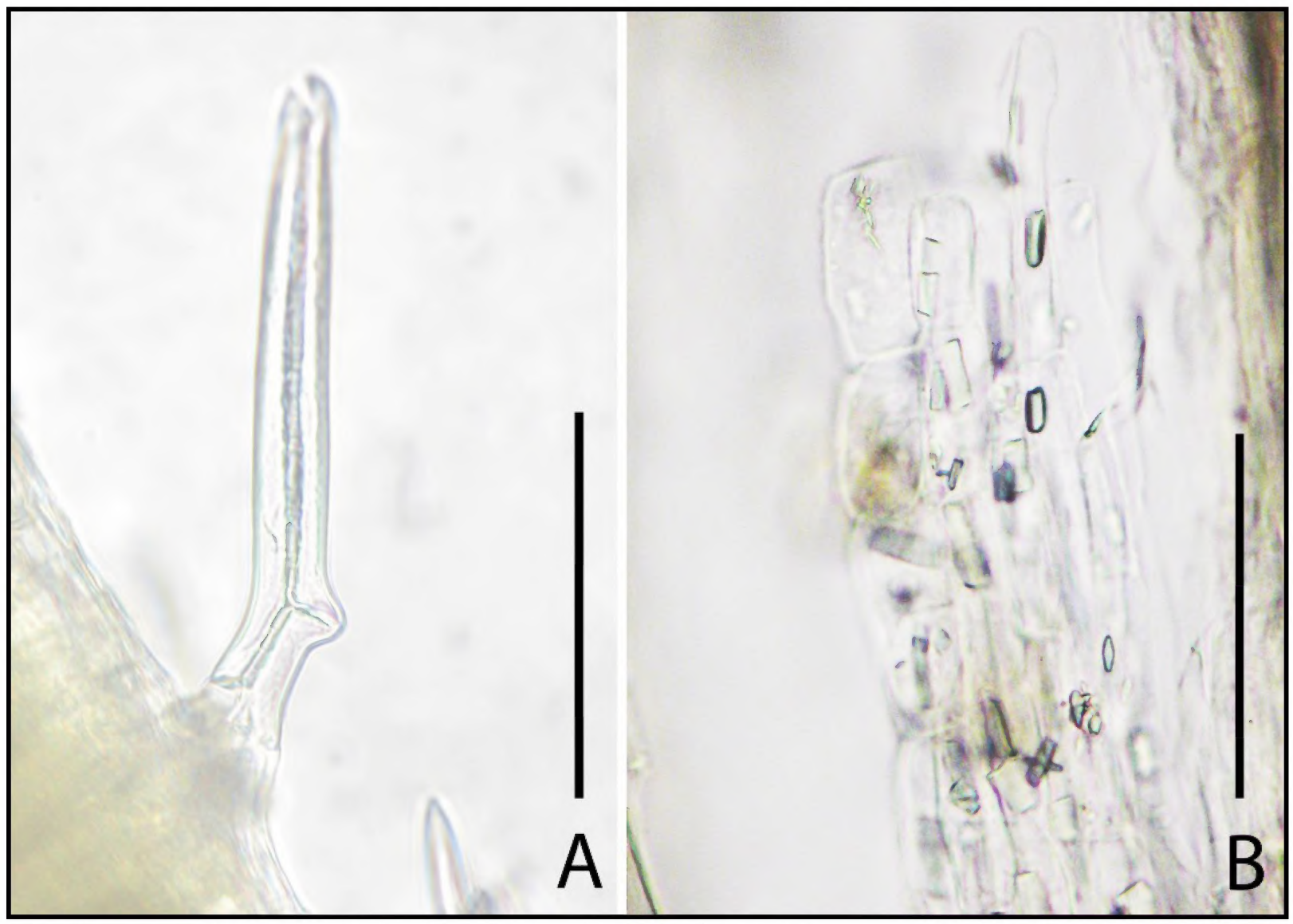

Figure 9. Cypsela microcharacters of *Bishopanthus werffii*. A. Duplex trichome. B. Pericarp showing several short-hexagonal raphide crystals. (From the holotype, *van der Werff et al. 25642*, MO). Scale bars A 0.5 mm, B 100 µm.

Distribution and ecology. *Bishopanthus werffii* (Fig. 2) is known only from the type locality, this west of Chachapoyas on the road to the Sarcofagos de Karajia (Depto. Amazonas, Peru). This shrub was collected between 2000–3000 meters elevation, and was in full flower in November. In April–July 2018 we searched for *B. werffii* at the type locality west of Chachapoyas along the road

to Karajia, and found instead the related *Ferreyranthus*. The type locality of *B. werffii* is only about 20 km north of the type locality of the nearly sympatric *B. soliceps* H. Rob. (Fig. 1), which was collected in flower in January. Similarly, during our hunts for *B. soliceps* south of Chachapoyas at the type locality near Tingo and Kuélap, we failed to find it and found instead only *Ferreyranthus*. *Bishopanthus* is apparently rare, and may remain narrowly endemic in Amazonas, Peru, occurring only east of the Río Marañon and south of the Huancabamba Depression. Although our searches were later than the known flowering season of *Bishopanthus* (November–January), it seems that neither species of *Bishopanthus* is as common as those of the related *Ferreyranthus*. About fourteen of the ca. 19 genera of Liabeae occur in Peru (Robinson 1983a, 1983b; Dillon & Sagástegui 1994; Gutiérrez 2010; Funk et al. 2012; Pruski 2012), with most centered in northern Peru, and so it is not altogether surprising to find a second species of *Bishopanthus* in the area where the tribe is especially well diversified. It is somewhat unsettling, however, that *Bishopanthus* contains two species, each known from only their respective types.

Bishopanthus werffii has leaf surfaces more or less smooth (never obviously bullate) adaxially and an open-cymose-corymbiform paucicapitulate (vs. solitary-capitulate) capitulescence, thus stands at odds with some features used as characteristic of *Bishopanthus* in the previous keys (e.g., Gutiérrez 2010; Robinson & Funk 2011). We do not know whether the lacerate enations on the clinanthium of *B. werffii* distinguish it from *B. soliceps*. Although the relatively well-spaced nodes and paucicapitulate branches seen in *B. werffii* (viz Figs. 5–6) are characters perhaps accentuated by year-to-year climatic differences, elsewhere within individual species of tribe Liabeae we have not seen such wide swings in morphology. It seems as though the gross structural differences seen in the types of each species of *Bishopanthus* are effectively constant, rather than (wholly) environmentally-induced. The nearly smooth (vs. adaxially bullate; compare Figs. 5A, 6 vs. Fig.1) leaves, fewer-flowered capitula, and non-setose (vs. proximally setose) corolla bases (compare Figs. 7A–C 8B; vs. Fig. 3E–F in Funk et al. 2013) of *B. werffii* further distinguish it from *B. soliceps*. We do not believe that the van der Werff collection is simply an extreme ecological variant of *B. soliceps*, the generitype, nor do we believe it should be placed in *Ferreyranthus*. Thus, we report the rediscovery of the genus *Bishopanthus*, and describe a second species, *Bishopanthus werffii*.

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